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CONTRIBUTIONS

FROM THE

ANATOMICAL LABORATORY

II

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PREFACE

The papers which are collected in this second volume of Contributions have been prepared by officers or students in the Department of Comparative Anatomy, and have recently appeared in various scientific journals. In the Table of Contents and on the title page of each separate paper will be found the place and time of publication.

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THE IMPORTANCE OF EXTENDED SCIENTIFIC INVESTIGATION.

By H. C. BUMPUS.

U. S. Fish Commission Bulletin for 1897.

THE IMPORTANCE OF EXTENDED SCIENTIFIC INVESTIGATION.

By H. C. BUMPUS, Ph. D.,
Professor of Comparative Anatomy, Brown University.

We meet here as members of a government that within less than three decades has not only revolutionized the methods of fish-culture, but has preserved to its several States, inland as well as seaboard, an industry yielding an annual income of over $45,000,000; a government which now maintains for the propagation of its fishes a fleet of steam and sailing vessels, more than a score of liberally equipped hatching and breeding stations, and which gratuitously issues to those unable to inspect its work a series of publications of great value to practical fishermen, of vast importance to the fish-culturist, and of sterling worth to the scientific world. The names of Baird, Verrill, Goode, and Ryder are familiar in every college and university, and their well-worn publications are conspicuous in biological laboratories from Italy to Scandinavia, and from Liverpool to Tokyo. Abstracts from reports of the United States Fish Commission form a considerable proportion of the last annual of the British laboratory at Plymouth, England, and other governments have frequently sent commissioners to inspect our hatcheries and acquaint themselves with American methods of work.

We should be careful, however, lest the consciousness of a successful past act as a sedative for the present. The lines of research wisely indicated by the founders, I might rather say founder, of American fish-culture should be assiduously followed, and the bypaths explored. The excellent reports of the one lately in charge of the Division of Fishery Methods and Statistics of the Commission—the secretary of this Congress—give an annual guarantee of the work actually accomplished and prove beyond peradventure that the Commission is not only self-supporting, but that the fisheries under its assistance are of rapidly increasing importance.

The introduction of the shad into the Pacific has yielded an average income of approximately $20,000, and the shad industry of the Atlantic, an industry yielding $2,000,000 annually, owes its continuance, if not also its existence, to the efforts of the United States Fish Commission. The planting of cod fry upon the coast of New England has replenished the waters of the east, and it is a fact that the fish were so plentiful in Narragansett Bay during the past autumn that nets could not be drawn, and the neighboring markets became overstocked.

The intelligent propagation of the cod rests upon the scientific work of Professor Ryder. Successful shad raising is largely due to the researches and devices of Commissioner McDonald. The life-history of the oyster was practically unknown until worked out by Professor Brooks. The migrations of the menhaden were unexplained before the researches of Dr. Peck. The work of Professor Libbey bears directly upon the question of distribution of the mackerel, and I venture to predict that successful sponge-culture will follow upon the continuation of the work begun at Woods Hole by Prof. H. V. Wilson. A continuance of these and similar lines of research is an absolute necessity for the growth and development of the more immediately practical work of propagation and distribution.

The collection and distribution of seeds is not the only function of the Department of Agriculture. This Department maintains a corps of scientific workers at home and abroad, and there is not a State, county, town, or hamlet that is not directly benefited by the results of its organized system of acquiring and diffusing knowledge. The efforts of the United States Fish Commission have been along similar lines and have yielded grand results, but the possibilities of the development of the fish industry have scarcely been indicated.

For some years the starfish have wrought havoc among the oysters of the colder water of our coast. The fishermen have laboriously "mopped" the "beds" with tangles of cotton waste, but have remained quite ignorant of the life habits of their enemy. A brief scientific study of the subject, however, has revealed many facts which point toward a possible, if not a probable, early correction of the evil. It has been found that the young, almost microscopic, gather in a narrow band along the shore, hidden in the eelgrass, where they may be killed off by the thousand with little labor and slight expense. Each oysterman, quite unwittingly, has been actually supporting, immediately around his oyster-bed, a nursery for the propagation of his enemy, the starfish.

In one direction in particular there is crying need of both extended and extensive scientific research. I refer to a matter that received some attention at the Chicago congress, namely, that research which shall result in the *development of the market* for food-fish. I think I do not overstate the fact when I say that there should be three times as much fish consumed as is consumed at the present time. The problem is not alone how shall we produce more fish, but how shall we improve the industry by providing a better and a more stable market for what is already produced. I feel that the fisherman and the fish-dealer are in a measure responsible for the fact that the average American can not endure fish oftener than one day in seven, and were it not for a wise provision of the church perhaps one day in seven would be far too frequent. While the dressing and shipping of meat and poultry has become almost an art, the methods of dressing and handling fish are crude in the extreme.

The abuse of fish as an article of food begins at the moment it is captured and extends to, and often beyond, the kitchen. I need not relate the rough handling on board the smack, the careless packing, and the slovenly condition of our markets; these are all prejudicial to the consumer as well as to the fish; but I wish to emphasize the fact that they are also sources of great loss to the dealer.

The blood that is ordinarily allowed to remain in the fish is the very medium that the bacteriologist uses for the culture of microbes, and its retention in the body of the fish provides the very medium in which the germs of decay delight. Should the fisherman bleed the fish immediately on its capture he would do much toward its reaching the consumer in a healthy condition.

The digestive organs of the fish are very active, and its processes of digestion continue after death; but while before death the contents of the alimentary tract are alone acted upon, after death the digestive ferments attack the surrounding tissues, and they attack these tissues with great energy. A few minutes is often sufficient for the deterioration of the flesh immediately inclosing the abdominal cavity. It would be a great saving to the dealer if the fish could be disemboweled and thoroughly washed as soon as captured.

Decay is practically an infectious disease. It is the direct result of the activity of certain microscopic organisms. If these organisms have difficulty in entering the tissue of the fish, or if their activity is inhibited through the application of cold or certain chemicals, the process of decay is retarded. Every time a fish is roughly handled, thrown upon the deck or pitched about as so much offal, walked upon or bruised in any way, the continuity of its flesh is broken and decay germs flood into the rupture. The slightest bruise of an apple or pear results in the formation of a center of decay quite visible to the eye. In the fish the center of decay is not so easily detected by the eye, but it is nevertheless present, and its presence is damaging to the dealer and disappointing to the consumer.

Animal tissue absorbs water very readily, but on the absorption of water it changes its structure, loses its flavor, and rapidly deteriorates. Fish should not be allowed to lie in their own slime on wet floors, or in poorly drained barrels and boxes.

The present method of shipping fish by the use of chopped ice is crude, expensive, and often ineffectual. Poultry, meat, or anything but a fish would find no market if shipped in a similar way. The fish arrive at their destination in a thoroughly uninviting condition, they are reeking with slime and filth, ghastly to the sight, offensive to the smell, and disgusting to the touch.

If the retailer, along the coast as well as inland, can be provided with fish that have been properly killed, skillfully cleaned, and carefully handled he will be in a position to present them to his customers in an attractive form, and the consumer will discover that all fish do not taste alike, which is synonymous with saying, all fish are not equally bad.

While urging that all lines of research already undertaken by the Government should be continued, I would suggest that a definite series of experiments be instituted which shall ascertain the best methods of preparing, packing, shipping, storing, and retailing fish, for I am convinced that improvements are possible along all these lines, and that with improvement the demand for food-fish will be very materially increased. Such an investigation, moreover, is eminently appropriate to the United States Fish Commission, since private enterprise can not be expected to experiment unselfishly for the public good.

This opens up another question: When more improved methods have been devised, how shall these, as well as the innumerable improved methods already familiar to the Commission, be brought to the attention of the fisherman?

There is no school, academy, or college, to my knowledge, in the entire United States which gives even one short course in the economics of fish-culture. There are, however, over 1,000,000 men, women, and children dependent upon the fisheries for their existence. The importance of providing instruction in practical fishery has already resulted in the establishment of schools in Norway, Sweden, Germany, and Japan. Dr. J. Lawrence-Hamilton has indicated the scope and outlined the courses for a Fisherfolk's Free Technical School in England, and the late Professor Goode urged the establishment of similar schools in this country. Though the first purpose of such a school should be to instruct, its laboratory would provide opportunities for research, its field equipment would stimulate investigation, and its existence would guarantee the collection and preservation of scientific data that would be of incalculable value to the fisherman as well as to the dealer.

It is a fact that at present there is not a single institution along our entire coast where one can observe the habits of our marine animals uninterruptedly throughout the year. There is no place where our biologists may go for a few weeks during the winter or early spring, when the ocean is teeming with animal life. The summer months are as the autumn to marine forms, and he who would study ocean life at its best must work in the early spring. The organization or individual that accomplishes the establishment of a permanent institution where instruction in practical fish-culture and fishery economics can be given; where apparatus is provided for the investigation of the lakes, rivers, and sea: where naturalists from our universities and commissioners from our States will be welcome at all times of the year, and where problems of scientific and economic interest can be studied and solved, will obtain what Baird, Goode, and Ryder saw in the distant future, and will combine and control the purely practical and the purely scientific. The need of American biology to day is the same as the need of successful fish culture—coordination, cooperation, and the establishment of a station, or the devotion of a station already established, like that at Woods Hole, to instruction and to extended uninterrupted scientific research.

PROVIDENCE, RHODE ISLAND.

THE ORIGIN AND BEHAVIOR OF THE CENTROSOMES IN THE ANNELID EGG.

By A. D. MEAD.

Journal of Morphology, Vol. XIV, No. 2.

THE ORIGIN AND BEHAVIOR

OF THE

Centrosomes in the Annelid Egg

BY

A. D. MEAD

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THE ORIGIN AND BEHAVIOR OF THE CENTROSOMES IN THE ANNELID EGG.

A. D. MEAD.

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I. GENERAL.

No protoplasmic structure has been the object of greater interest or incited more investigation during the last few years than the centrosome. The fact that it remained undiscovered until a comparatively recent date, and that, with modern technique, it has been found to occur in cells representing many different tissues in a variety of animals and plants, would alone place the centrosome in a conspicuous position in the literature on the cell; but the difficulty and uncertainty often attending the demonstration of this structure, its minuteness, the variety of phases under which it manifests itself, the diversity and supreme importance of the functions attributed to it, either as the bearer of hereditary qualities or as the organizer and director of cell-activities, have stimulated research and discussion to an extraordinary degree.

The literature on the centrosome has developed two general problems toward the solution of which the results of these observations are contributed.

(a) *The Morphological Relation of the Centrosome to the Other Organs of the Cell.*

This problem demands consideration of the doubt as to the very *existence* of the centrosome as a definite cell-organ, and of the uncertainty as to the *identity* of this organ in case it exists.

The possibility that bodies described as centrosomes are frequently artifacts does not rest solely upon the negative evidence of numerous observers who fail to find centrosomes where they might be expected to occur, but upon the fact that similar bodies can be produced by the coagulative action of certain reagents.

The classic centrosomes, which dance the quadrille in the egg of *Strongylocentrotus lividus* (Fol, '91) are not found by later workers in the eggs of closely related sea-urchins. In his first paper on the "Fertilization of Toxopneustes," Wilson maintains that in well-preserved material "there is absolutely nothing to be identified as a centrosome," though irregular clumps — fortuitous groups of granules — closely similar to those described by Fol as "centrosomes" may be produced by the destructive action of picro-osmic acid. Eismond (*Anat. Anz.*, X, 7, 8) and others have suggested that the centrosomes or "centrioles" have been, at least in some cases, produced by the clotting action of reagents, and do not represent actual cell-organs. But in view of the fact that so many investigators have demonstrated the centrosome in many different cells and with different reagents, and that in some instances this structure can be followed through a constant and continuous series of changes, including growth and division, it is safe to maintain that the centrosome is an actual organ of the cell.

While the existence of the centrosome has been established beyond a reasonable doubt, there still remains the puzzling question of *identity*. Structures widely different in appearance have been called centrosomes, and the same structure has been designated by this and by various other names. Much confusion, therefore, arises from the terminology, though the discrepances can by no means be assigned to this cause alone, for there are differences of interpretation in regard to the morphological limitations of the structure itself.

Watasé's endeavor to bring into relation the various protoplasmic structures, cyto-microsomes, "centrosomes," *Zwischenkörper*, rod-like "centrosomes" of the pigment-cell, contraction-band of the muscle-cell etc., is an attempt to extend, not the terminology, but the homology of the centrosome. Which of the three concentric structures — centrosphere, centrosome, or centriole — at the centre of the aster in Echinus (Boveri) is the morphological equivalent of the centrosomes of Strongylocentrotus (Fol), the large centrosphere of Toxopneustes (Wilson), the scattered centrosomes in the leucocyte (Heidenhain), the centrosphere-like centrosomes of Crepidula (Conklin), the minute centrosomes of Myzostoma (Wheeler), Chætopterus (Mead), and Thalassema (Griffin), must, terminology aside, remain a matter of interpretation based on structural and physiological characters.

It is usually assumed that that structure in the aster which persists through the various stages of mitosis is to be considered the centrosome, whether it be a large reticular area (Crepidula), a minute dot frequently surrounded by such an area, or a structure midway between the two (Echinus). On this principle Wilson, in his paper on the "Archoplasm, Centrosome, and Chromatin of the Sea-urchin Egg," raises his previously described "central mass" of the aster of Toxopneustes to the morphological value of a centrosome, though he has since, on other grounds, altered this interpretation. "What, then, shall we identify in the sperm-aster of Toxopneustes as the 'centrosome' in Boveri's sense, *i.e.*, as the structure that divides to form the dynamic centres of the ensuing cleavage? I think the only structure that can answer to this definition is the central mass of the aster, *i.e.*, the substance of the original middle-piece, without regard to its subsequent morphological differentiation."

It was on precisely these grounds that, in a preliminary paper on the "Fecundation of Chætopterus," I identified the minute dark granules in the centres of the asters as centrosomes, and endeavored to show that the centrosomes which were developed in connection with the sperm-aster persist and, by successive divisions, furnish the centrosomes of each cleavage-spindle up to the 8-cell stage. Having requested some of my preparations for examination, Wilson says in referring to them (*Atlas of Fertilization*, p. 20): "The central mass of the aster undoubtedly contains at this period (early phase of the cleavage-amphiaster) one or two deeply staining centrioles, which in this case may possibly have the morphological value of centrosomes." However, reëxamination of all the stages with new material supports my earlier interpretation that these structures have unquestionably the morphological value of centrosomes.

More recently Wilson also has discovered two deeply staining "centrioles" in the aster of the egg of the annelid Nereis, and Griffin, working under his direction, has found the same in Thalassema. Griffin has also showed that these granules, arising in the sperm-aster, persist through the first cleavage-amphiaster, divide and give rise to the centrosomes of the succeeding amphiasters. In view of these results, which indicate that "the true centrosome certainly corresponds to the central granule or centriole," Wilson is inclined to modify again his interpretation of the identity of the centrosome, and to believe that further research will bring out the "minute central centrosome" in Toxopneustes, and in all similar cases where they appear to be absent.

I am indebted to Dr. F. R. Lillie for permission to refer to some extremely interesting unpublished observations on the egg-centrosomes of Unio which, doubtless, will throw a great deal of light upon the question of *identity*. From the stage in which it has the appearance of a minute, deeply staining dot, the centrosome is traced, step by step, through a metamorphosis in many of whose phases its identity would not ordinarily be recognized.

The problem of the morphological relation of the centrosome to the other organs of the cell involves also the important questions of its origin and its persistence. This question, both sides of which have the support of eminent authority, has been stated by Watasé ('94) in the following terms: "According to the one view (1) the centrosome is a permanent or ultimate organ of the cell, an organ *sui generis*, and coexistent with other organs of the cell, as the nucleus and the cytoplasm. According to the other view (2) the centrosome is a derivative structure, arising by the modification of some preëxisting element in the cell, as the chromosome, nucleolus, or the cytoplasm."

The theory that the centrosome is a permanent and ultimate organ of the cell finds direct support in the observations of a number of investigators, which prove beyond doubt that the centrosome is capable of self-division and growth, and that it may persist from one generation to another.

In Chætopterus the centrosomes can be seen distinctly in every phase of mitosis, and are always surrounded by an aster, even in the resting stage. On the other hand, in certain animals, the centrosomes are not always demonstrable in the asters. Sometimes both the asters and the centrosomes vanish for a while and then reappear (Wheeler, Lillie, MacFarland, etc.). It is conceivable, however, that, though invisible, the centrosomes may be present in the cell, for they have been found to lie naked in the cytoplasm, bereft of rays (Heidenhain, '93).

To maintain that the centrosomes are absent, simply because they are not demonstrable, is, of course, to base an assumption upon negative evidence, a procedure especially dangerous when applied to the centrosome, inasmuch as this structure is, at best, very minute, and comparatively difficult to demonstrate, even when its exact position is indicated by the presence of an aster.

But, admitting that the centrosome is "a persistent morphological element having the power of growth, division, and persistence in the daughter cells," and even admitting that it exists incognito, it remains to be proved that it arises only by division from a preëxisting centrosome and that it does not cease to exist as a morphological element in cells which subsequently possess centrosomes.

Watasé has pointed out that the transition between centrosomes and other structures of the cytoplasm should be sought, not among the most highly developed typical centrosomes, such as are to be found in mitosis, but among structures — centrosomes or homologues of centrosomes — which are less persistent and pass more easily from one phase into another; for example, the *Zwischenkörper* and the contraction-band in muscle-cells.

But the origin and behavior of the asters and centrosomes in the maturation of Chætopterus directly support the interpretation that the centrosomes arise *de novo* out of the cytoplasm and are resolved into it, and that they are not, therefore, permanent organs of the cell, like the chromosomes, although some of them show a considerable degree of persistence.

Leading up to the formation of the first maturation-amphiaster, there are formed within the egg a large number of distinct asters (seventy-five more or less), two of which — the primary — come to lie at the poles of the maturation-spindle.[1] The view held by the majority of recent workers that the aster is "formed under the influence of the centrosome," or the admission that the centrosome is in any way a constant feature or necessary adjunct of the aster (and without this hypothesis there is no force in the permanent-organ theory) offers a dilemma: either (*a*) this cell (the oöcyte of the first order) contains a very large number of centrosomes which have arisen by the division of a preceding centrosome, or (*b*) it contains a large number of centrosomes which have arisen *de novo* out of the cytoplasm. If one accepts the first alternative, he must imagine a satisfactory explanation of the origin of the many centrosomes from a preceding element of the same kind, and of their distribution to the various portions of the cytoplasm, and must also account for the total disappearance of by far the larger portion of them. It is hard to reconcile such wholesale disappearance with the notion of the centrosome as a permanent and ultimate organ of the cell.

Multiple asters, similar to those in Chætopterus, have been described by Carnoy in Ascaris during the formation of the second polar globule, and by Reinke ('94) in the peritoneal cells of the larval salamander. Reinke groups the multiple asters into three classes, — primary, secondary, and tertiary mechanical centres, — according to the degree of their development. The primary mechanical centres, which contain a true centrosome, arise by the coalescence and further development of the secondary and these in turn arise in a similar manner from the tertiary centres. Watasé has seen in the egg of Macrobdella "a series of thirteen asters, ranging from a miniature aster, with a microsome for its centre, to the normal aster, with a veritable centrosome."

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[1] Possibly several coalesce to form each aster (see p. 195).

Morgan ('96) found numerous "artificial astrospheres" in sea-urchin eggs kept in sea-water to which 1½% salt had been added. The salt, he believes, stimulates the living eggs to produce these structures. It is interesting that the multiple asters appear in the eggs of Chætopterus immediately after they have been deposited in sea-water. The latter probably contains more salt than the fluids of the body-cavity of the worm.

R. Hertwig ('95) has shown that minute quantities of strichnine stimulate the production of asters (even amphiasters) in the maturated unfertilized egg of the sea-urchin. No centrosomes, however, were found.

Osterhout ('97) has recently described in Equisetum the origin of the amphiaster from multiple asters, though no centrosomes were demonstrable. In the egg of Unio, during the metaphase of the second maturation-spindle, a supernumerary aster appears, remains for a short period, and then vanishes. The interesting question presents itself, — If this supernumerary aster contains a centrosome, from what preceding centrosome does it arise? If it does not contain a centrosome, the latter is not a necessary feature, much less the originator, of the aster.

Referring to the observations of Reinke, Watasé, Morgan, and Hertwig, Wilson says: "All these observations are of high interest in their bearing on the historical origin of the centrosome; but they do not prove that the centrosome of the normal aster ever arises by free formation. On the whole, the evidence has steadily increased that the centrosome is to be classed among the permanent cell-organs; but whether it ranks with the nucleus in this regard must be left an open question" ("Cell," p. 226).[1]

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[1] In the appendix to the second edition of this book on the "Cell," Wilson is inclined to adopt a conclusion nearly related to that which he maintained in an earlier paper ('95), by reason of recent observations which "throw grave doubts upon the hypothesis of the universal autonomy and genetic continuity of the centrosome."

The multiple asters in the egg of Chætopterus are certainly normal; they are demonstrable in the *living eggs*, are brought out by various reagents, are a constant feature of every egg at a certain stage of its development, and always undergo a constant and continuous series of consecutive changes. Therefore, as far as the phenomena in Chætopterus prove the free formation of the centrosome at all, they prove it in the normal aster; and the same can be said of Reinke's observation.

(b) *The Function of the Centrosomes in Fertilization.*

The classic papers of Boveri ('87, '91) and Fol ('91) formulated and brought into prominence two distinct theories of fertilization: that of Boveri rests upon the supposition that the centrosome is the dynamic centre of the cell and initiates cell-activities. It implies also that the centrosome is a permanent and ultimate cell-organ, handed down from one generation to another by means of the spermatozoön. The gist of the theory appears in a paragraph from his earlier paper: "The ripe eggs possess all the organs and qualities necessary for division, excepting the centrosome, by which division is initiated. The spermatozoön, on the other hand, is provided with a centrosome, but lacks the substance in which this organ of division may exert its activity. Through the union of the two cells in fertilization, all the essential organs necessary for division are brought together; the egg now contains a centrosome which, by its own division, leads the way in the embryonic development." He writes also: "The end of fertilization is the union of the germ nuclei and the equal distribution of their substance, while the active agent in this process is the centrosome. . . . It is the centrosome alone that causes the division of the egg, and is, therefore, the fertilizing element proper." To these conclusions Wilson subscribes.[1]

Fol maintained, on the other hand, that, in fertilization, the centrosomes of the cleavage-amphiaster arise by the fusion of sperm-centrosomes and egg-centrosomes, just as the cleavage-nucleus is formed by the union of the sperm-nucleus and the egg-nucleus. The centrosome at either pole of the amphiaster is composed of both male and female elements; for the original sperm-centrosome and egg-centrosome divide into two, and each daughter-centrosome derived from the sperm fuses with one of the daughter-centrosomes derived from the egg. The obvious inference which has been drawn from these phenomena is that "fertilization consists, not only in the adding together of the two pronuclei derived from individuals of different sexes, but also in the fusion of four half-centres derived from the father and the mother into two new bodies, the astrocentres" (centrosomes).[1] Obviously, if the permanent presence and fusion of the sperm- and egg-nuclei indicate that these structures are the vehicles of hereditary properties, the same function may be predicated of the centrosomes.

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[1] Wilson, "The Cell," p. 140.

The results of Guignard's researches on the fertilization of the lily and Conklin's work on the gasteropod Crepidula agree in all essential respects with those of Fol on the sea-urchin. According to almost every other observer, however, either the sperm-centrosome or the egg-centrosome, or both, disappear before the formation of the cleavage-amphiaster — a phenomenon manifestly incompatible with Fol's interpretation of their functions in fertilization. The fusion of the sperm- and egg-centrosomes in fertilization is not of universal occurrence, and the inference that these structures are vehicles for the conveyance of hereditary qualities is unwarranted.

But the observations which discredit Fol's interpretation do not confirm, in every case, Boveri's theory of fertilization. Wheeler showed that in Myzostoma there is no indication that a centrosome is brought in by the spermatozoön or that a centrosome or aster subsequently develops in connection with the sperm-nucleus. On the other hand, the egg-centrosomes derived from the second maturation-spindle accompany the egg-pronucleus as it approaches that of the sperm. During the approach of the pronuclei the egg-centrosomes move away from each other as though they were to form the poles of the cleavage-amphiaster; but during a certain brief period "it is extremely difficult or even impossible to make out the egg-centrosomes." It is probable that these bodies — certainly not the sperm-centrosomes — enter into the formation of the first cleavage-spindle.

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[1] Fol (**'91**), p. 274; Conklin (**'94**), p. 18.

Miss Foot's ('97) account of the origin of the cleavage-centrosomes in *Allolobophora fœtida* does not accord with Boveri's theory of fertilization nor with that of Fol. "The egg attraction sphere is present during the two maturation divisions, but after the second polar body is formed and the female pronucleus begins to develop it totally disappears. The sperm attraction sphere is present until the head of the spermatozoön begins to develop into the male pronucleus, when it also totally disappears. Both spheres are absent during a relatively long period (*i.e.*, while the growing pronuclei are developing); and when the two pronuclei have attained their maximum size and are in contact, two attraction spheres again appear in the cytoplasm and the cleavage-spindle is formed."

Lillie ('97) has observed a peculiar behavior of the centrosomes and asters in Unio. After undergoing extraordinary metamorphoses, the egg-centrosomes alone enter into the formation of the cleavage-amphiaster, as they do in Myzostoma; a conspicuous comet-like aster with a centrosome develops in connection with the sperm-nucleus, but totally disappears before the pronuclei come together.

MacFarland's ('97) results on Pleurophyllidia are similar to those of Miss Foot on Allolobophora in that both egg- and sperm-centres are apparently absent during a certain period preceding the union of the pronuclei.

All these observations form a serious obstacle in the way of accepting Boveri's theory of fertilization, but there is a further and perhaps more serious difficulty in the insecurity of the hypotheses underlying the theory itself; *viz.*, (*a*) that the centrosome is a permanent organ of the cell, and (*b*) that it initiates and directs the cell-activities. We have already referred to the question of the validity of the first of these hypotheses (p. 185), and comparison of the normal fertilization phenomena of various forms leaves room for doubt as to the validity of the second. The eggs of various animals attain to different stages of maturation before fertilization takes place; some remain in the germinal-vesicle stage (with no visible centrosome or aster) and await the entrance of the spermatozoön (Nereis), some remain in the metaphase of the first maturation-amphiaster (Chætopterus), while others proceed with the formation of the polar globules and the reconstitution of the egg-nucleus before fertilization (sea-urchin). If it is the function of the centrosomes upon being brought into the egg "to organize the machinery of mitotic division,"[1] its task must be very different in different eggs; for in one it must first organize the machinery for the two maturation-divisions, in another it finds this machinery already organized but in a state of rest, and in a third it has to organize only the machinery for the first cleavage-mitosis.

In Chætopterus the behavior of the sperm-centrosomes is strictly orthodox, according to Boveri's doctrine ; they are the centrosomes of the first cleavage-spindle, and give rise by division to those of the succeeding spindles, while the egg-centrosomes totally disappear. Nevertheless, it does not seem necessary to conclude that it is by virtue of the presence of the sperm-centrosomes, rather than of the sperm-nucleus, that the maturation-processes are resumed, even if we grant that the spermatozoön brings in the centrosomes. An adequate demonstration that the sperm-centrosomes are actually carried into the egg by the entering sperm is, moreover, extremely difficult to make, and it is perfectly possible, as Miss Foot has urged, that in many cases these structures arise *de novo* out of the egg-cytoplasm in the *vicinity* of the middle-piece of the spermatozoön.

The foregoing considerations lead to the conclusion that the centrosomes in fertilization are neither vehicles of hereditary qualities nor the active agents which organize the machinery of mitotic division, but that they may be, like other centrosomes, "the expression rather than the cause of cell-activities."

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[1] Wilson, "The Cell," p. 171.

II. Descriptive.

(a) *Collection and Preparation of Material.*

The observations recorded in the following pages were made upon the eggs of *Chæptopterus pergamentaceus* Cuvier, procured at the Marine Biological Laboratory, Woods Holl, Mass., during the summers of 1894, 1896, and 1897.

These extraordinary annelids are found below low-water mark in leathery tubes. The latter are U-shaped, ten to fifteen inches long, about an inch in diameter in the widest part, and are buried beneath the mud except half an inch at either end. After being removed from the tubes the animals may be kept alive for a few days in an aquarium; they are quite helpless in their new environment, and usually lie on their side, keeping up continuously the rhythmical respiratory movement of their wing-like body-folds, which, under natural conditions, would serve to create currents of water through the tubes. When disturbed at night, they emit a phosphorescent light, apparently dependent upon a secretion from epidermal glands, for the water in which they have been kept becomes itself slightly phosphorescent.

The sexes are readily distinguished, the body-wall being nearly transparent and the posterior segments distended with eggs or spermatozoa. The large parapodia hold the sexual products, and any number may be cut off without injury to the worm. The eggs may be fertilized at any time during the day or night and will develop normally, provided the sperm is added within a few hours after they have been removed from the ovaries. This is true of every individual collected during the months of July and August, and indicates that the eggs are probably carried in the body for many days after they are perfectly mature and ready to be fertilized. If the eggs are kept in sea-water for half an hour or more and not fertilized, all except the smaller ovarian eggs are found to have the first maturation-spindle well formed, in its definitive position, and always in the same stage of development, *i.e.*, the metaphase or equatorial-plate stage. But, if the eggs are examined after having remained *only a few minutes* in sea-water, they are all found to contain the germinal vesicle and no spindle. It is evident, therefore, that sea-water in some way stimulates the eggs to the production of the maturation-spindles.

(b) *Method of Fixing and Staining.*

The best preparations were obtained by fixing the eggs in Boveri's picro-acetic acid, and staining with Heidenhain's iron-alum hæmatoxylin, followed by orange G. The slides were left in 4% iron-alum for half an hour, rinsed, and left in ½% hæmatoxylin for twelve hours. After drawing the color with iron-alum, the slides were dipped in an aqueous solution of orange G or Bordeaux red. Hermann's fluid, Flemming's fluid, and a mixture of Hermann and formalin also gave satisfactory results, though the staining was not so brilliant. Sublimate-acetic usually wrought havoc in the region of the centrosphere, though the astral rays were not destroyed. The sections varied in thickness from three to seven and one-half microns.

(c) *Origin of the Maturation-Spindle.*

The figures in Plate I represent sections of the unfertilized eggs during the growing-period and up to the formation of the first maturation-spindle. As may be seen in Fig. 1, the smaller eggs lie nearest the lumen of the ovarian tubule. They are characterized by their relatively large nuclei and their compact cytoplasm which stains, throughout the egg, a nearly uniform deep purple (Pl. XVI, Figs. 1, *a*, *b*, and 2).

The older eggs, usually more remote from the lumen of the tubule, are larger, the increase in size being due in great measure to the accumulation of yolk, the distribution of which is accompanied by noteworthy changes in the appearance of the cytoplasm. The latter takes on the appearance of a reticulum composed of beaded strands which stain purple, while within the meshes lie the pale yellow yolk-granules. Up to the time when the egg has attained about two-thirds its full size, only a part of the protoplasm presents the loose reticular appearance; the rest remains as dark purple masses, which I consider to be equivalent to the *nebenkerne* or paranuclei of various authors (Fig. 1, *c*, *d*, *f*). These masses are not homogeneous, but resolve themselves into a cytoplasmic network, of which the meshes are much compressed, and the strands usually parallel with the surface of the nucleus, though at the periphery of the masses they fray out and become continuous with the open network which contains the yolk (Fig. 1, *g*, Fig. 3, *par.n.*, Fig. 4, *par.n.*). Frequently sections show but one mass of this sort, crescentic in outline, with the concavity toward the nucleus, and occasionally some of the constituent fibres, instead of running parallel with the nucleus, are rolled up spirally. As a rule, however, the paranucleus is fragmented and numerous portions are found in a zone between the nucleus and the periphery of the egg. The substance within the meshes of the paranuclear reticulum does not take the yellow, but the blue or the purple stain.

As the egg accumulates more yolk and increases in size, the paranuclei, through a process of continuous ravelling, become resolved into the network which now presents a nearly uniform appearance throughout the cytoplasm. The last traces of the fragmented paranucleus are recognizable even when composed of only two or three strands (Fig. 4). The reticulum can be traced with ease to the extreme periphery, where it forms what, in section, appears to be a distinct beaded line, running entirely around the egg. Immediately inside this outer "pellicle" is a narrow zone containing a single layer of yolk-granules regularly arranged (Fig. 9), and in this zone the strands of the cytoplasm are comparatively few. The nuclear membrane is continuous with the cytoreticulum and presents a similar granular appearance. During the growth of the ovum the character of the reticulum is constantly changing in respect both to the shape of the meshes and to the thickness of the component strands. In later phases of the paranucleus, and immediately after its disappearance, the reticulum is particularly easy to demonstrate. The strands are, at this time, thick, richly stained, and seem to be composed of a series of granules arranged in linear order, while the meshes are small and, in section, nearly circular in outline.

But although the structure of the reticulum, the peripheral egg membrane (pellicle), and the nuclear membrane are easily demonstrable and beautifully clear throughout the cytoplasm, there is, as yet, *no trace of anything suggesting a centrosome or an aster.* As the egg grows larger, however, the outlines of the meshes become polygonal rather than circular (Fig. 6), and show rather pronounced nodes. Eggs which have reached this stage of development, when placed in sea-water continue to develop as far as the formation of the first maturation-spindle. The tendency of the fibrils of the network to straighten becomes accentuated, so that many of them extend in straight lines for a distance several times the diameter of the single meshes (Fig. 6). Moreover, these longer fibrils radiate from common centres, and in this way there arise in the cytoplasm a number of *miniature asters* (Figs. 6, 7). At first the asters possess only two or three rays, but the latter soon increase in number and in length at the direct expense of the remaining network. The formation of asters continues until a climax is reached, when one can count no less than seventy-five distinct asters scattered about through the cytoplasm of a single egg. They are most numerous in the zone formerly occupied by the paranucleus. These structures correspond closely to the "secondary mechanical centres" of Reinke, and, for reasons which appear further on, I have called them *secondary asters*.[1]

All stages in the development of the asters out of the polygonal network may be represented in a single section, yet often many of the larger asters are approximately equal in size, and, though distinct from one another, are frequently so close together that their rays intercross (Fig. 7). The nuclear membrane now presents a peculiar appearance, being drawn out into numerous sharp points — a phenomenon which is probably correlated with the development of the multiple asters (Fig. 7).

The period of development characterized by the multiple asters is not of long duration. Two of the asters gain predominance over the others in point of size, and continue to grow larger, while the others gradually evanesce (Fig. 8).

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[1] Mead ('97a).

These two primary asters ("primary mechanical centres," Reinke, '94) arise at some distance from the wall of the germinal vesicle, and usually about ninety degrees from each other, though they may be nearer together or even farther apart. I am not prepared to say at present whether the primary asters are formed by the further growth and specialization of two of the secondary asters or by the union and coalescence of several.

The nuclear membrane regains its regular contour when the multiple asters have vanished, except for a deep sinus in the vicinity of each of the two primary asters (Figs. 8, 9). A well-defined centrosome, staining dark brown, now appears in the centre of each aster, surrounded by an area of lighter color (centrosphere) from which the large granular astral rays diverge in all directions. *These are the centrosomes and asters of the first maturation-spindle* (Figs. 9–13). The centrosphere always stains brown, though very much lighter than the centrosome. The rays from the two asters give the appearance of actually pushing in the nuclear membrane, though the latter remains for a while intact.

The rays of the two primary asters are many of them coarse and quite extensive (Fig. 9). They do not, however, reach the periphery, but break up into the network which extends throughout the whole cytoplasmic portion of the egg. Eventually the nuclear membrane disappears, though the region corresponding to the germinal vesicle still takes a stain different from the rest of the protoplasm and has also a different texture (Figs. 10, 11).

Between the two asters a spindle is formed which remains for some time near the vanishing germinal vesicle, but at right angles to the radius of the egg. The rays from the asters enter the region of the vesicle, the chromosomes gather at the equator of the spindle, and the latter gradually swings around to its definitive position, perpendicular to the surface of the egg (Figs. 10–13). The nucleolus, meantime, breaks up into a number of pieces which remain for a time in the vicinity of the spindle, but gradually degenerate and disappear. The centrosomes divide very early before the spindle begins to move toward the surface, and appear as two distinct dots in the midst of a clear yellow centrosphere at either end of the spindle.

The fibres of the central spindle differ in color from the other fibres of the asters, staining yellowish brown with orange G (or red with Bordeaux) much like the centrospheres, while the other rays are purplish. The chromosomes, moreover, do not, at first, lie directly between the two poles, but upon the surface of the central spindle (Fig. 10); later they seem to insinuate themselves between its fibres (Fig. 11).

The remains of the germinal vesicle are evident for some time after the spindle has assumed its definitive position, but gradually fade away (Figs. 12–15). Having reached the metaphase the spindle remains without apparent change until the egg is fertilized. The astral rays extend for a long distance into the cytoplasm, intercross with one another, and break up at the ends into the cytoreticulum, which is now much more delicate and finer than during the earlier stages when the paranucleus was disappearing.

It is difficult to understand why the process of karyokinesis should be suspended at this time, for the apparatus of division is apparently ready, the asters are well developed, the chromosomes in position at the equator of the spindle, and the centrosomes have divided in anticipation of the next mitosis (Figs. 13–16).

(d) *Observations upon the Unfertilized Living Eggs.*

During the past summer I have examined a large number of living eggs to confirm the results obtained from the study of preserved material. Full-grown eggs taken from the body-cavity of the female and examined under slight pressure invariably show a germinal vesicle with even contour, and inside the vesicle the nucleolus. The cytoplasm is, at first, uniformly opaque, but in two or three minutes a number of light points appear, and soon the whole cytoplasm is studded with a multitude of *secondary asters*. Since the yolk is repelled from the centre of the asters, the latter appear as transparent spots in an opaque field. After about four minutes two of the asters (primary asters) become especially distinct and the others gradually evanesce. The two arise separately, sometimes near together, sometimes far apart.

When one of these living primary asters is examined under a high power, the yolk-granules can be seen to move away from the centre with a trembling, vibratory motion. Later the areas free from yolk extend to the region between the two asters, which represents the central spindle, and within about ten minutes after the egg is placed in sea-water the whole amphiaster migrates to its definitive position at the periphery of the egg.

The changes in the contour of the germinal vesicle and its final disappearance can also be followed in the living egg. All these phenomena afford a complete confirmation of the results already obtained from the study of preserved material.

(e) *Fertilization.*

The spermatozoön of Chætopterus has a bullet-shaped head and a long vibratile tail. When first teased out into sea-water, it remains motionless for a few minutes, but soon becomes extremely active. Apparently it may penetrate the egg at any point on the surface, though it usually enters nearer the vegetative pole. Polyspermy is rare. The entrance of the spermatozoön initiates profound changes in all parts of the egg. The latent activity of the maturation-amphiaster is revived; the polar globules and the female pronucleus are formed while the sperm is but a very minute and inconspicuous body in a distant portion of the egg.

Other changes are begun in the vicinity of the spermatozoön itself. After it has penetrated a little distance, a diminutive aster with two centrosomes lying close together and surrounded by a minute centrosphere may be seen near it (Fig. 19). These two centrosomes are the sperm-centrosomes, though in Chætopterus I am not sure that they are actually carried in by the spermatozoön. However this may be, the sperm-centrosomes separate as the head of the spermatozoön enlarges to form the male pronucleus, and, as they separate, the rays diverging from them become more and more extensive (Figs. 21, 22, 25, 30, 31, 34, 36–38).

Besides moving apart, the centrosomes migrate toward the centre of the egg, the male pronucleus accompanying them, sometimes on one side and sometimes on another, but always near at hand. Their final position is near the centre of the egg, on the side toward the polar globules. The central spindle, which has developed between them, lies at right angles to the egg-axis (Figs. 30, 36–38). After the centrosomes have separated a certain distance, the centrosphere disappears and the rays diverge from the centrosomes themselves. A lightly staining band—the incipient central spindle of the first cleavage-amphiaster — extends from one centrosome to the other (Figs. 36–39).

The rays of the sperm-asters become more and more extensive at the expense of the cytoreticulum until, at the time of the union of the pronuclei, they often extend to the extreme periphery and incorporate nearly all the cytoplasm of the egg. They are not straight but curved, those from either centrosome taking different directions, so that in certain portions of the egg the rays cross one another (Figs. 36–40).

Since the central spindle and two centres of radiation lie on one side of the male pronucleus and in close proximity to it, a conical space on the opposite side of the pronucleus is left free from the rays (Figs. 38–40). In this space and between the rays in other portions of the egg, especially near the periphery, strands of cytoplasm may be seen running in various directions (Figs. 39, 40). The rays themselves are usually branched at the outer ends. The yolk-granules do not approach very near to the centres of radiation, apparently because the rays are too numerous or because the asters repel them. A few granules, however, are found in the conical space opposite the amphiaster and near the pronucleus (Fig. 38).

The sperm-head, or male pronucleus, having grown to its full size, finally takes a slightly eccentric position in that radius of the egg which, if extended, would pass through the polar globules, while near it lie the male centrosomes and the huge amphiaster just described (Figs. 34–40).[1]

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[1] In the late stages (Figs. 36–38) there are variations in the relative position of the male pronucleus and amphiaster which show a certain degree of independence

While these phenomena, directly connected with the development of the male pronucleus and amphiaster, have been going on, the first maturation-amphiaster, whose activity was resumed upon the entrance of the spermatozoön, has brought about an apparently independent series of changes in another part of the egg resulting in the formation of the polar globules.

Beginning with the formation of the polar globules, the living egg undergoes a constant series of form changes, these being most pronounced in eggs taken from worms which have been but a short time (one or two days) in the aquarium. While the first polar globule is being formed, the egg, at first spherical, becomes distinctly flattened at the animal pole. This reminds one of the flattening of the adjacent surfaces of the cleavage-blastomeres which occurs shortly after cell-division.

The egg resumes its spherical form, but, after the extrusion of the second polar globule, becomes pear-shaped, the smaller end at the animal pole. It again assumes for a short time the form of a sphere. A protuberance then appears upon the vegetative hemisphere. The successive stages in the development of this protuberance — *yolk-lobe* — are uniformly synchronous with the various phases of the first cleavage-mitosis.[1] The lobe first becomes noticeable during the early metaphase of the spindle, and reaches the height of its development during the telophase. Meanwhile, the first cleavage-furrow cuts the egg into two unequal cells and the lobe remains attached to the larger one, into which it is later resorbed. These phenomena are of especial interest in connection with certain experiments which I have made upon unfertilized eggs.

Soon after the maturation-spindle resumes its activity the nine chromosomes divide and the daughter-chromosomes migrate toward the two poles of the spindle, while the double centrosomes at the inner end of the spindle move apart and a small central spindle is formed between them (Figs. 14–20). The centrosphere fades away and the rays diverge directly from the two centres, as was the case in the evolution of the sperm-

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in the behavior of both; but, notwithstanding these variations, the axis of the amphiaster is in every case at right angles to the egg-axis.

[1] The same is true of the yolk-lobe in mollusks; *cf.* Crampton.

amphiaster at a corresponding stage. The centrosomes at the *outer* end, however, do not move further apart, but are carried into the first polar globule with the nine daughter-chromosomes, and there degenerate (Figs. 19–21).

During the early phases of mitosis the amphiaster presents several interesting features. The yellowish brown fibres of the central spindle may be seen between the chromosomes after they have divided. Between the halves of each chromosome is a distinct white band with no such fibres, but a few minutely beaded, almost black lines (Fig. 17). The spindle does not taper to a point at either end, but is truncated, and at the truncated ends a ring of extremely minute dots, like the centrosomes in color but very much smaller, are brought out in many of the clearest preparations (Figs. 14, 15). These dots are probably nine in number and appear to be the foci of pencils of rays extending to the chromosomes. The latter are clearly seen in transverse sections of the spindle at a little distance from the equator.

In the very late stages of mitosis a delicate *Zwischenkörper* is formed at the junction of the polar globule and egg, but it soon vanishes and has nothing to do with the formation of the second maturation-spindle.

The daughter-chromosomes at the inner end of the spindle, which at first lie in a circle, later take on an elliptical arrangement, while the adjacent centrosomes continue to move apart and eventually lie one at either end of the ellipse (Figs. 22–24). The central spindle, which was formed between the two centrosomes at a very early stage, has now reached considerable size, and we have the incipient amphiaster of the second maturation-spindle.

The centrosomes at the poles of this aster are identical with the two which lie close together at the inner end of the first maturation-spindle (Figs. 14–17), and these are derived by division from one of the centrosomes of the primary asters (Figs. 8–13). The chromosomes soon are drawn into the equator of the spindle, and the latter gradually swings around to a position vertical or nearly so, directly under the first polar globule (Figs. 25–29). Again, a centrosphere develops around each centrosome, and the rays of the aster — which have never been absent — diverge from it, rather than directly from the centrosome. The centrosome at the inner end of the spindle often, perhaps always, divides, but the daughter-centrosomes are not so large as the corresponding ones in the first spindle, and always remain close together (Figs. 28, 29).

The chromosomes, during the metaphase of the second maturation-amphiaster, are frequently dumb-bell shaped (Figs. 26, 27), and sometimes in four parts, as shown in Fig. 28. The succeeding phases are similar to those of the first maturation-amphiaster described above. The peculiar "wake" left in the midst of the fibres of the central spindle by the receding halves of the chromosomes is evident during the anaphase, and by this means one can ascertain which of the daughter-chromosomes were together (Fig. 29). It is found in some instances that one of the chromosomes is drawn much nearer the pole of the spindle than its counterpart.[1]

The second polar globule is formed directly under the first, which is thus pushed away (Figs. 31–33), and it contains the centrosomes and the nine daughter-chromosomes (Fig. 31).

At about the 32-cell stage, both polar globules are ingested by the apical cells.[2] The *Zwischenkörper*, which is developed during this mitosis, persists for a considerable time, as may be seen by comparing Figs. 31, 32, 35, 37, and 39.

As the spindle vanishes the chromosomes which were at the inner end elongate and bend so as to become V-shaped (Figs. 31–33). They then group themselves in a hollow hemisphere whose concave side is directed toward the centre of the egg so as partially to obscure the centrosome and its vaguely defined centrosphere, though at this period the radiations from the aster in question are extensive and very distinct, many of them crossing those of the male aster. The chromosomes ultimately surround the centrosome so that the astral rays diverge from their very midst (Figs. 33–35).

Gradually the chromosomes become vesiculated and, as the nine vesicles begin to migrate toward the male pronucleus, they continue to grow and press against one another, still including the female centrosome, whose position is indicated by the point of convergence of the rays (Figs. 35–38). The latter gradually become fewer and less distinct and finally vanish altogether. I believe that the rays of the female aster, which were so strongly developed in the earlier stages of the reconstitution of the pronucleus, become resolved into a cytoplasmic network, which in part may be incorporated into the system of rays belonging to the male amphiaster. I have seen during this period of disintegration a number of extremely minute asters (secondary or tertiary mechanical centres) between the periphery of the egg and the female pronucleus.

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[1] In this figure the lithographer has slightly displaced the outer centrosomes and the chromosome nearest the pole.

[2] *Cf.* Mead, '97b.

The vesicles completely coalesce to form a female pronucleus similar in size and general appearance to the male pronucleus with which it later comes into close apposition (Fig. 39).

These phenomena suggest the interpretation that the chromosomes at the inner pole of the second maturation-spindle are not only drawn toward the egg-centre, but that the latter continues for some time to be the centre of attraction and thus groups the chromosomic vesicles about itself and holds them together. The disappearance of the female aster is simultaneous with the coalescence of the vesicles. After their fusion there is no further need of this attractive influence and the aster disappears. Apparently, also, the male centres exert an attractive influence upon the group of vesicles as a whole, though it is not ordinarily strong enough to dissociate the group by drawing the nearest vesicles to the centre in advance of the others. In one case, however, this phenomenon seems actually to take place (Fig. 36).

But, whether the grouping of the vesicles is a function of the female centrosome or not, it would seem utterly preposterous to presume that this waning structure suddenly emerges from the midst of the fusing vesicles, divides, and unites with the male centrosomes.

Before the two pronuclei meet, the vesicles of the female are completely united and resemble the male pronucleus in all respects, though they always lie on the side toward the polar globules. The two pronuclei come together and flatten against each other between the poles of the male amphiaster, forming a spherical nucleus — the first cleavage-nucleus (Figs. 39, 40).[1]

The male asters reach the height of their development as the pronuclei come together, and the two centres, connected by a spindle, are already widely separated. Each centre contains a clearly defined and easily demonstrable centrosome, which is soon surrounded by an incipient centrosphere, from which the protoplasmic rays extend throughout the whole egg (Figs. 39, 40). The pronuclei elongate, while the poles of the spindle continue to move further apart, and later the nuclear membrane gradually disappears. An actual fusion of the pronuclei does not take place (Figs. 40, 41), and, even after the membrane has vanished, the chromosomes derived from the egg and from the spermatozoön respectively are often seen to be in separate groups (Fig. 43). As the cleavage-nucleus begins to elongate, the rays of the amphiaster become less extensive, breaking up into a network in the outer portion of the cytoplasm, and when the nuclear membrane disappears, centrospheres become more strongly developed around the centrosomes. The chromosomes arrange themselves in an equatorial plate, and the metaphase of the first cleavage-amphiaster is established (Figs. 43, 44).

The centrosomes at the poles of the spindle by this time have each divided in anticipation of the next mitosis, and the centrospheres have increased in size. Several nucleoli lie scattered among the chromosomes in the equatorial plate (Fig. 45). Like the chromosomes they stain with hæmatoxylin, but are easily distinguished by their irregular shape and arrangement (Fig. 46).

The chromosomes split longitudinally according to the heterotypical method (Figs. 44, 45), and the daughter-chromosomes recede toward the opposite poles (Fig. 46). In the cross-section of the spindle I have often counted the chromosomes, and found them always to be eighteen in number (Fig. 47), as would be expected, since there were nine in the maturation-spindle (Fig. 18). When the daughter-chromosomes have separated to some distance, the nucleoli are seen in their original position midway between the poles of the spindle (Figs. 46,

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[1] The signs ♂ and ♀ in Figs. 40, 41, and 43 should be transposed.

46^a), where they remain during the succeeding stages of mitosis (Figs. 48–52).

The centrospheres reach their greatest development toward the end of the anaphase, though the radiations at this time are not so extensive (Figs. 46^a–48). The centrosomes, which divided very early, continually move apart within the centrosphere without in the least altering the regular contour of the latter. In the early stages a line joining the two centrosomes would nearly coincide with the spindle-axis, but as they move apart they also swing around through an angle of about 90° (Figs. 44–48). The distance between the centrosomes within the centrosphere is in definite and constant relation to the successive phases of mitosis, and one can predict the position of the chromosomes from the examination of the centrosomes, and *vice versa.* The centrosphere is smaller in the end of the spindle which belongs to the smaller cell (Figs. 46, 46^a, 48). The dark brown centrosomes are especially distinct during these stages in contrast to the light yellow centrosphere. In some preparations a minute halo surrounds each centrosome (Fig. 46), and in the later stages of the anaphase, before the centrosome disappears, a band of fibres, the incipient central spindle of the next mitosis, is demonstrable between them (Figs. 46^a, 47).

When the rod-like chromosomes have reached a position near the centrosphere they gradually become vesiculated. Each chromosome at first appears as a double row of granules, separated by a longitudinal cleft (Fig. 48), but later the regular arrangement of the granules is lost, and each chromosome continues to swell up and forms an oval vesicle (Fig. 49) resembling a miniature nucleus. I have several times counted the vesicles, and always found them to be eighteen. They arrange themselves in the form of a disc, and for some time the fibres of the centrosphere may be seen between them (Fig. 49). As they grow still larger they coalesce, not into a single mass, but into several irregular masses which themselves fuse to form a spherical nucleus (Figs. 50, 51).

The cytoplasmic portion of the egg becomes constricted during the later phases of the reconstitution of the nuclei, and in the line between the two new cells there appears a series of black granules, the foci of pencils of connecting fibres extending in both directions to the nuclei (Fig. 51). These bodies later become aggregated at one place and form a large brown *Zwischenkörper* (staining like a centrosome), from which the rays diverge. In side view the *Zwischenkörper* may always be seen to lie below a line connecting the centres of the nuclei; *i.e.*, nearer the vegetative pole. At this stage the nucleolar fragments of the original cleavage-nucleus lie in the larger of the two cells (Figs. 51, 52). Here they remain for a while, gradually becoming smaller and less distinct, and vanish entirely before the karyokinetic figures are formed in the two blastomeres.

The centrosomes, which divided at an early stage and separated as the karyokinesis progressed, continue to move apart during the reconstitution of the nuclei, and a spindle develops between each pair. While the chromosomes are being transformed into vesicles the centrosphere at either end of the spindle disappears (Fig. 49), and the rays which now diverge from the centrosomes increase rapidly in length and thickness, and reach their maximum development in a late stage of the reconstitution of the nucleus, as is represented in Figs. 51 and 52. They extend to the periphery of the egg and are easily distinguishable between the closely packed yolk-granules at the lower pole. They can be traced even through the substance of the yolk-lobe which develops on the lower hemisphere when the first cleavage-spindle is in an early stage (metaphase) and eventually becomes a part of the larger of the two blastomeres (see Fig. 50).[1] The rays diminish in extent as the new nucleus assumes its definitive spherical contour; the centrosomes, meanwhile, take their respective positions, nearly 180° apart, near the surface of the nucleus (Fig. 53).

The reconstitution of the nuclei and the accompanying phenomena proceed simultaneously in the two blastomeres, and each is now in a stage of karyokinesis exactly comparable to that of the original oösperm after the union of the pronuclei.

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[1] In a previous account of this phenomenon I said that the yolk-lobe was separated from the blastomere. This was a mistake, which I corrected in a later paper.

One cycle of karyokinesis has been completed, and the next cycle which is concluded with the formation of the four blastomeres is essentially similar. Around each centrosome there develops a centrosphere (Fig. 53). The nuclear membrane, beginning at the portion nearest the centrosome, breaks down (Fig. 54), the chromosomes group themselves in the equatorial plate (Figs. 55, 56), and the typical anaphase is established. During the succeeding stages, the chromosomes in each blastomere divide longitudinally and migrate toward the poles of the spindle, the nucleoli drop out into the cytoplasm, and the centrosomes divide and move apart within the growing centrosphere (Figs. 57, 58).

I have followed the karyokinetic processes to the formation of sixteen cells. All the phenomena are essentially similar to those in the preceding cycles of division. The thirty-two centrosomes of the 16-cell stage arise by the successive divisions of the original sperm-centrosome, while the centrospheres, on the other hand, appear and vanish in each mitosis.

III. Summary.

During the growing-period of the oöcytes a deeply-staining paranucleus is developed which contains a reticulum continuous with that of the surrounding cytoplasm; but, before the oöcyte has attained to its full size, this structure becomes entirely resorbed into the general cytoreticulum.

Ripe eggs may be carried in the body-cavity of the worm for several days before they are laid. During this time neither centrosome nor aster can be distinguished, though the reticulum is unusually distinct. In a few minutes after the eggs have been deposited in sea-water, however, a large number of asters are developed by rearrangement of the cytoplasmic network.

Two of these asters (primary asters) continue to develop and finally lie at the poles of the first maturation-spindle, while the others gradually vanish. Distinct centrosomes are not demonstrable except in the primary asters. If they are present in the multiple asters, it is extremely difficult to reconcile their presence with the theory that the centrosome is a permanent cell-organ; for the theory would require, in this instance, that no less than seventy-five centrosomes should arise by the division of the two centrosomes of the cell of the preceding generation, and that these centrosomes should be distributed throughout the larger portion of the egg-cytoplasm. If they are not present in these asters, the centrosomes are only an occasional and not a constant or an essential feature of the aster.

The centrosomes of the two primary asters evidently arise *de novo* out of the cytoplasm, and are typical in every respect; they lie in the midst of the astrospheres, grow, divide, and persist in the next cell-generation.

Normally the maturation of the unfertilized egg proceeds no further than the metaphase of the first maturation-spindle, but upon the entrance of the spermatozoön the karyokinetic activity is immediately resumed and the maturation is completed. I do not know whether the spermatozoön actually brings the sperm-centrosomes into the egg or not; at any rate, they are demonstrable in the midst of a minute aster which lies close to the sperm-head soon after the latter enters. From this time the development of the sperm-aster into the cleavage-amphiaster, and the mitotic divisions resulting in the formation of the polar globules, proceed simultaneously in different parts of the egg, and appear to be independent phenomena.

The primary centrosomes lie at the poles of the first maturation-spindle, and the daughter-centrosomes, arising by the division of one of these, move apart and form the poles of the second maturation-spindle. During the reconstitution of the egg-nucleus and its approach to the sperm-nucleus, the egg-centrosome remains in the midst of the fusing vesicles, its position being indicated by the point of convergence of the rays of its waning aster. Not only the fact of its disappearance, but the fact that, when last seen, the centrosome is in the midst of the group of vesicles, renders it in the highest degree improbable that the egg-centrosome takes part in the formation of the cleavage-amphiaster. Moreover, the sperm-centrosomes may always be seen at the poles of the incipient cleavage-amphiaster, and they become more and more conspicuous up to the time of the fusion of the pronuclei. During the metaphase of the cleavage-amphiaster the sperm-centrosomes divide, and the daughter-centrosomes at either pole move apart (an incipient central spindle developing between them) and form the poles of the cleavage-spindles of the two blastomeres. This process is repeated in each subsequent mitosis, and the centrosome can be demonstrated, lying in the midst of an aster, at every phase of mitosis, even including the so-called "resting stage." It follows, therefore, that the centrosomes of the cleavage-cells are derived directly from the sperm-centrosomes, — a fact irreconcilable with Fol's theory of the "quadrille."

The behavior of the sperm-centrosomes is in harmony with Boveri's theory of fertilization, but is not necessarily a confirmation of it; for the karyokinetic activities which are revived upon the entrance of the sperm are those leading to the formation of the polar globules. The machinery for these mitotic divisions is already organized, and it is quite as likely that the stimulus which starts it going emanates from the sperm-nucleus as that it emanates from the sperm-centrosomes.

There are nine chromosomes in each maturation-amphiaster and eighteen in the cleavage-spindle. In the metaphase of each cleavage-amphiaster the numerous nucleoli lie scattered among the chromosomes and remain at the equator of the spindle until they completely degenerate. As mitosis progresses, the chromosomes split longitudinally and the halves move toward opposite poles of the spindle, where they form new nuclei.

During the telophase of each mitosis a distinct *Zwischenkörper* is present, which gradually fades away as the reconstituted nuclei approach the "resting stage."

It is a pleasure to acknowledge the many courtesies extended to me by Dr. Whitman and other officers of the Marine Biological Laboratory, and to express my appreciation of the kind assistance of my friend Dr. W. M. Wheeler.

Brown University,
September 26, 1897.

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EXPLANATION OF PLATE XVI.

Unfertilized ovarian eggs. Except where otherwise stated, the figures are drawn from single sections.

FIG. 1. Transverse section of ovarian tubule, showing relative size, position, and color of ova in different stages of development, *a–k*. Paranucleus in *c–g*. Beginning of formation of asters in *i* and *j*, which are well developed in *k*; *ep.o.*, outer epithelium of ovary; *ep.i.* inner epithelium.

FIG. 2. Small ovarian eggs, *a* and *b* of Fig. 1; same scale of magnification as rest of figures.

FIG. 3. Compare with stage *f* of Fig. 1; *par.n.*, paranucleus; *n.*, nucleolus.

FIG. 4. Last traces of the paranucleus.

FIG. 5. Slightly later stage than Fig. 4. Paranucleus has become completely resolved into the cytoreticulum; compare *h*, Fig. 1.

FIG. 6. The cytoplasmic network beginning to form small asters. On the right the pellicle is torn away from the rest of the reticulum. Compare *i* and *j*, Fig. 1.

FIG. 7. Numerous secondary asters at the height of their development. Compare *k*, Fig. 1.

FIG. 8. The two predominant primary asters with centrosomes. Beginning of the inpushing of nuclear membrane. Several small secondary asters still visible.

FIG. 9. Egg with only the two primary asters; each with a clear centrosome, (dark brown). Distinct inpushing of nuclear membrane. Eggs at this stage are no longer attached to the ovary.

FIG. 10. First maturation-spindle lying on the surface of the nucleus; nuclear membrane dissolved. Chromosomes and nucleolus outside the spindle; centrosomes in each aster doubled and smaller than in Fig. 9.

FIG. 11. Side view, similar to Fig. 10. Remains of germinal vesicle in middle of egg. The chromosomes, which appear in the drawing to be in the midst of the spindle, are seen by focusing to lie above the central spindle. In the right-hand aster only one centrosome is visible; the other is probably directly below it.

FIG. 12. Later; the spindle has swung around to a vertical position; *n.*, nucleolus; *ch.*, chromosomes. Both centrosomes are visible in the inner aster, one lying almost underneath the other, and therefore farther apart than they appear in the figure. The last remnants of the nucleus nuc.

FIG. 13. Chromosomes of more definite shape and more evenly distributed around the equator of the spindle. Spindle more elongated and nearer the periphery of the egg. Remains of nucleolus on the left.

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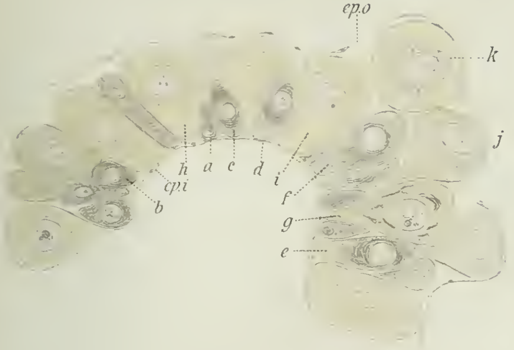

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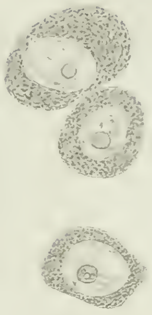

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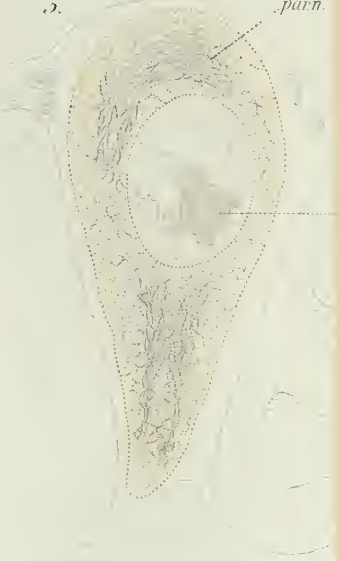

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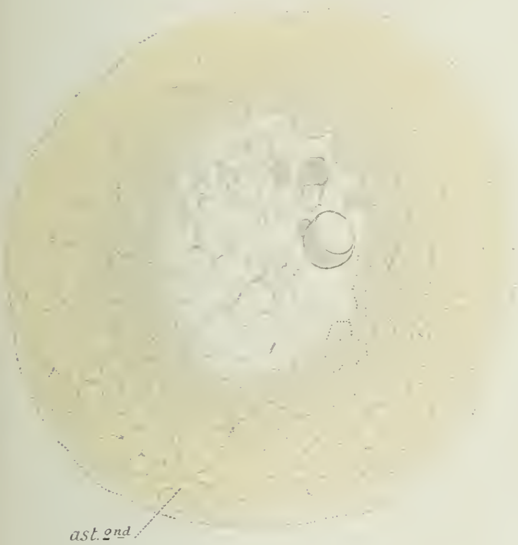

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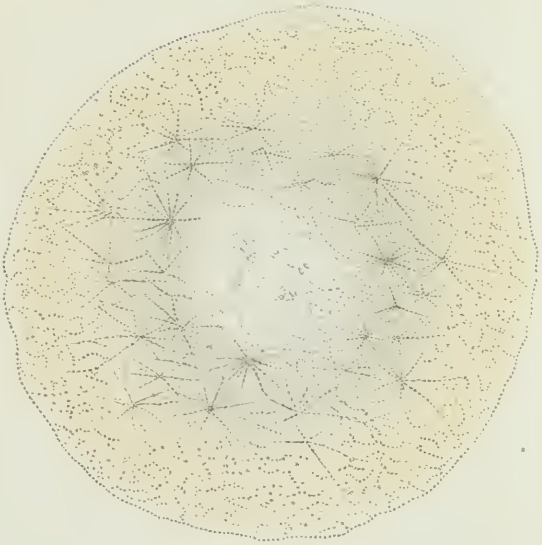

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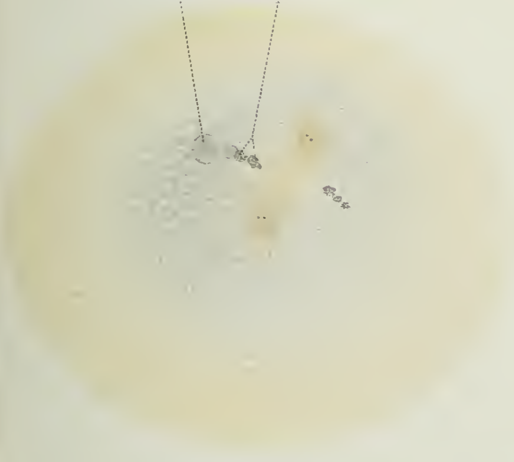

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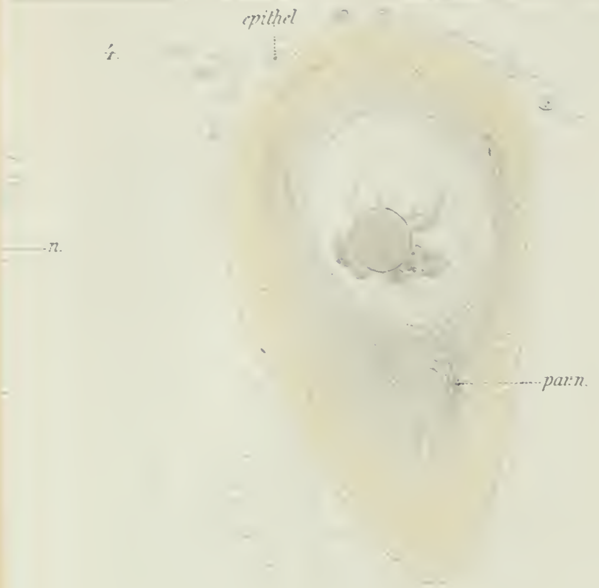

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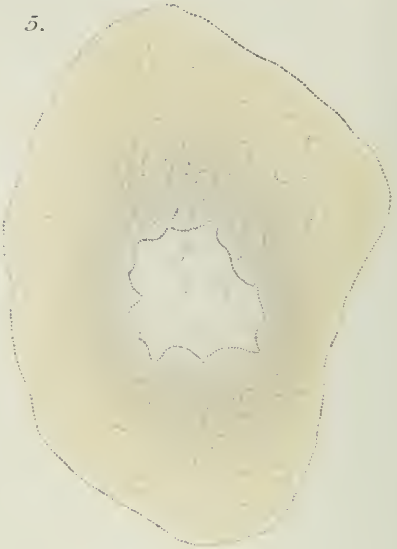

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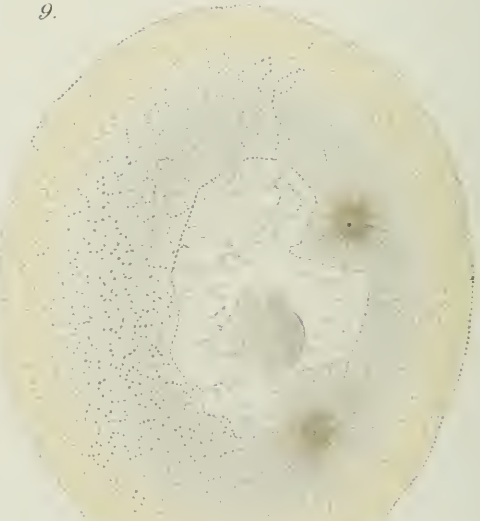

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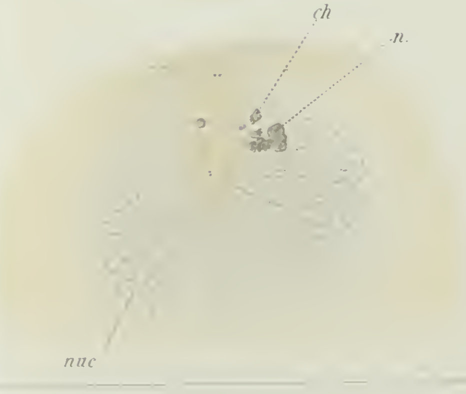

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Lith. Anst. v Werner & Winter, Frankfurt a/M.

EXPLANATION OF PLATE XVII.

With the possible exception of Figs. 14 to 16, all are fertilized.

Fig. 14. First maturation-spindle after the disappearance of nucleoli. Double centrosome in each end. Circle of dots around end of spindle. (Two sections combined.)

Fig. 15. Similar to Fig. 14; centrosomes of inner aster further apart; circle of dots more deeply stained.

Fig. 16. Circle of dots not brought out, though the centrosomes are clear. There are probably two centrosomes at the outer end of the spindle, though only one shows in this section.

Fig. 17. About ten minutes after fertilization. Daughter-chromosomes moving toward the pole of the spindle. The two centrosomes at the inner end of the spindle moving apart, showing a faint whitish band (not clear in the lithograph) between them.

Fig. 18. Transverse section through the equatorial plate, showing the nine chromosomes.

Fig. 19. First maturation-spindle in anaphase. Polar globule beginning to protrude. Young sperm-nucleus, ♀ with its single (?) centrosome.

Fig. 20. The first polar globule. One of the outer centrosomes of the first maturation-spindle degenerating, but still visible. The two inner centrosomes widely separated, with an incipient spindle between them. A mere suggestion of a *Zwischenkörper* in the large spindle, *z*. The sperm-nucleus as in Fig. 19. This figure shows the distinction in color between the blue-black chromosomes and the brown-black centrosomes which is always present in the preparations themselves. Sperm-nucleus from adjacent section.

Fig. 21. Oblique view; first polar globule, *Zwischenkörper*, male pronucleus with aster and two centrosomes. Remains of centrosome in the polar globule. Combined from several sections. The full number (9) of chromosomes in the egg.

Fig. 22. Oblique section; after the evanescence of the first maturation-spindle. Some of the chromosomes at inner end of the first spindle; compare Fig. 20. The two centrosomes more widely separated, between them the incipient central spindle; *p.g.*, polar globule in tangential section. Two sperm-centrosomes.

Fig. 23. Incipient second maturation-spindle; slightly later than Fig. 22, not all the chromosomes in this section.

Fig. 24. Two adjacent sections *a* and *b*; *p.g.*, first polar globule with chromosomes fusing together; second maturation-spindle far advanced.

Fig. 25. Second maturation-spindle beginning to swing around into vertical position. Sperm-nucleus with aster and two centrosomes.

Fig. 26. The second maturation-spindle in its final position. Aster of sperm-nucleus with extensive rays.

Fig. 27. Second maturation-spindle a little later.

Fig. 28. Same, with quadruple chromosomes. Circle of dots around end of spindle; compare Figs. 3, 14, and 15.

FIG. 29. Second maturation-spindle; compare Fig. 17. One chromosome near outer pole of the spindle. All the daughter-chromosomes can be seen in this section by focusing.

FIG. 30. A little later stage, paired sperm-centrosomes; whitish band between the two centrosomes. Centrosomes of maturation-spindle indistinct.

FIG. 31. Telophase of second maturation-spindle. Degenerating centrosomes in the second polar globule, *p.g.*^{2}; *Zwischenkörper*, *z.*; sperm-nucleus, ♂, with two centrosomes which are not so widely separated as in Fig. 30, though here the maturation processes are farther advanced (all one section 3μ).

FIG. 32. About the same stage; shows the more usual conditions in that the second polar globule, *p.g.*^{2} pushes the first away from egg. Egg membrane, *m*, ; *z. Zwischenkörper* or middle-plate.

FIG. 33. Later than Fig. 32. The chromosomes at inner end of second maturation-spindle in the form of loops and partly surrounding the centrosome and aster. It is possible that there are two centrosomes. The location of the centre of the aster is indicated by the point of convergence of the rays, which at this time are very prominent.

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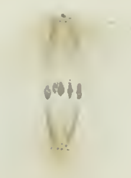

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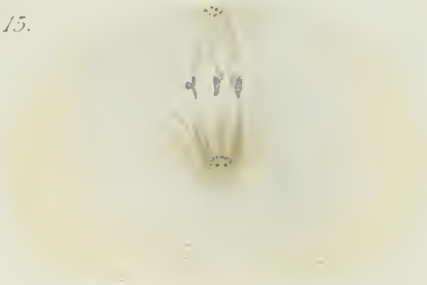

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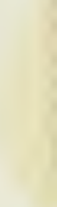

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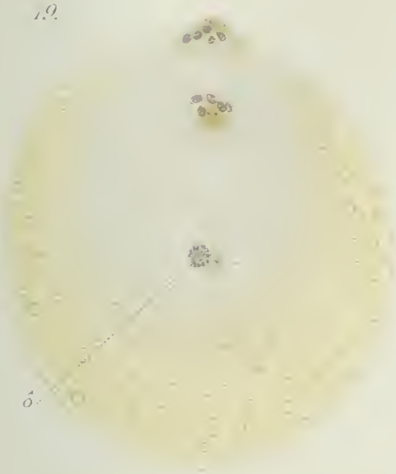

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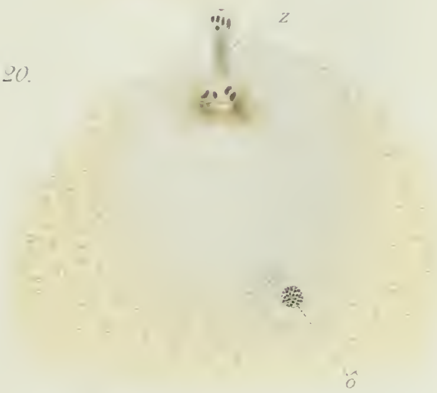

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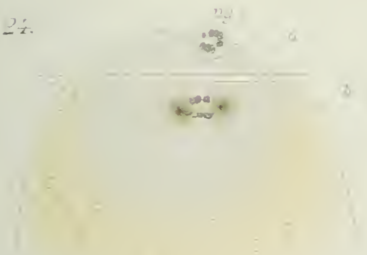

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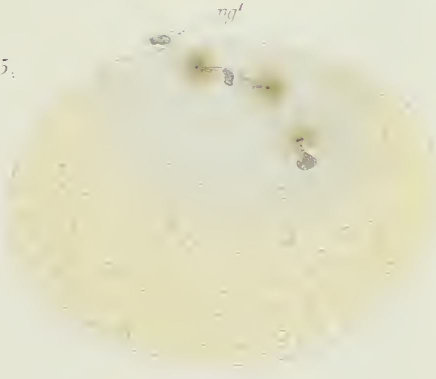

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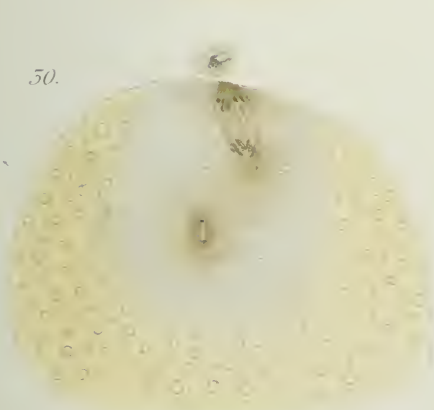

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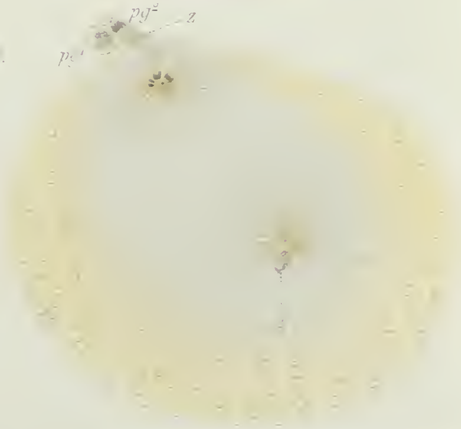

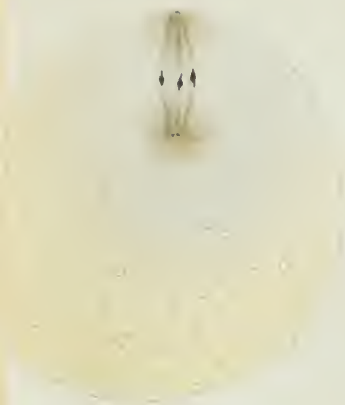

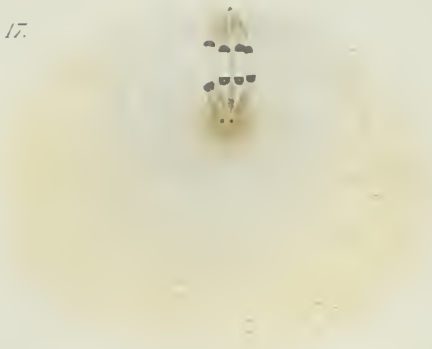

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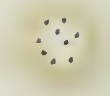

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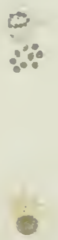

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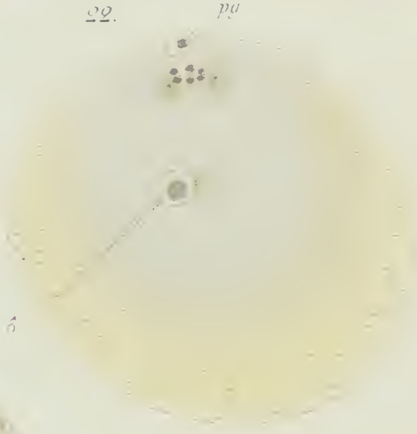

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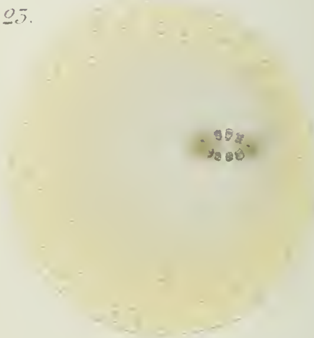

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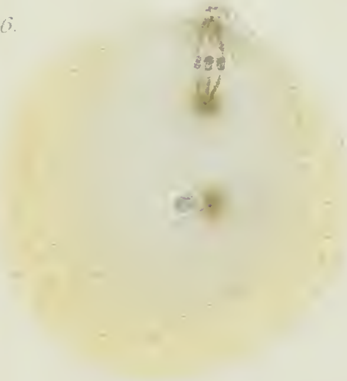

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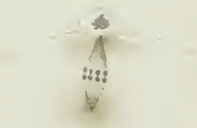

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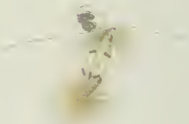

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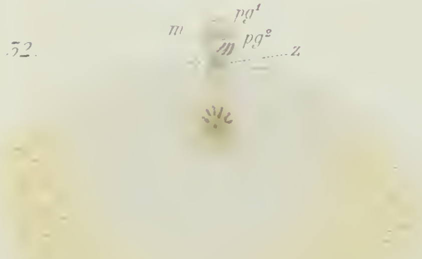

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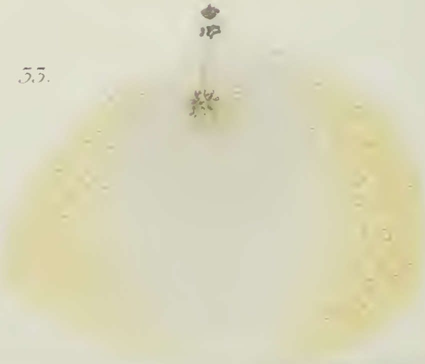

EXPLANATION OF PLATE XVIII.

FIG. 34. Two sections combined as indicated by the arcs of circles. First polar globule lost, second polar globule bent over. Male pronucleus and aster with two centrosomes in the centre of the egg.

FIG. 35. Two polar globules, *p.g.*[1] and *p.g.*[2]; *Zwischenkörper*, *z*. Cluster of vesicles, ♀, formed from chromosomes left in the egg after the second maturation-division. In the midst of the vesicles lies the centrosome towards which the rays converge. In the midst of the egg the male pronucleus and aster with one of the two centrosomes in sight (the other in the next section). The rays of both sperm and egg-asters break up near the periphery into the network.

FIG. 36. The two male asters with centrosomes and long rays are in definitive position; sperm-nucleus, ♂, in rather unusual position, *i.e.*, between asters and female pronucleus, the vesicles of which are larger than in preceding figure. Anomalous case of one vesicle reaching the male pronucleus before the others. Aster with rays (two sections combined).

FIG. 37. Two polar globules, 1 and 2; *Zwischenkörper*, *z*. Vesicles of female pronucleus very large and close together. Male pronucleus in rather unusual position at side of asters. Spindle between the latter. Rays of asters extend to the periphery and converge to the centrosomes themselves, as in preceding figure; no centrosphere.

FIG. 38. Later than Fig. 37. Vesicles of female pronucleus uniting, a few faint rays converging to their midst. Male pronucleus and asters in usual position. (Two sections combined.)

FIG. 39. Two polar globules, 1 and 2; *Zwischenkörper*, *z*. Male and female pronuclei about to unite. Two male centrosomes and asters. Female aster has entirely disappeared.

FIG. 40. Male and female pronuclei have united. The male asters on either side. Centrosomes are clear and centrospheres are beginning to form about them. The rays diverging from the latter are commencing to break up into a reticulum near the periphery. Round nucleoli in the pronuclei. Signs ♂ and ♀ transposed.

FIG. 41. First cleavage-nucleus elongated; its membrane commencing to break down at the ends. The two sperm-asters with centrosomes and centrospheres; rays comparatively short. Signs ♂ and ♀ transposed.

FIG. 42. Somewhat later stage. Mere traces of nuclear membrane now visible. Chromatin, nucleolus, *n.*, in middle, centrosomes and centrosphere larger than in preceding figure.

FIG. 43. Cleavage-spindle in metaphase. Chromatin in two clusters, and nucleoli scattered among the chromatin loops. Centrosome in right aster elongated in preparation for a division. Signs ♂ and ♀ transposed.

FIG. 44. Later stage. Centrospheres more highly developed; centrosomes dividing in anticipation of next cleavage.

FIG. 45. Daughter-chromosomes divided and beginning to migrate toward the two poles of the spindle, leaving nucleoli in the middle. Daughter-chromosomes moving apart.

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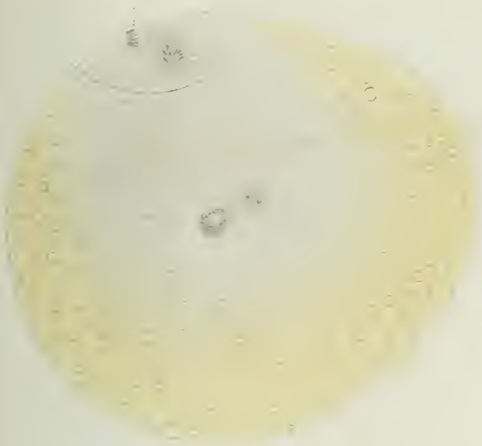

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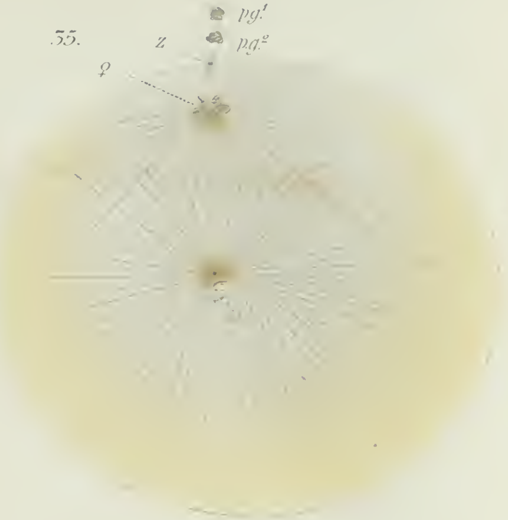

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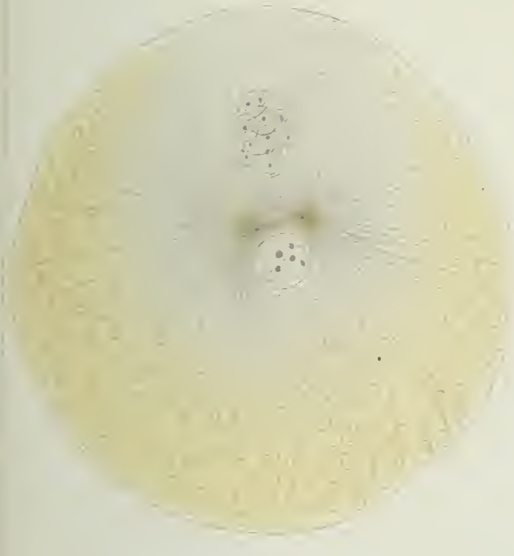

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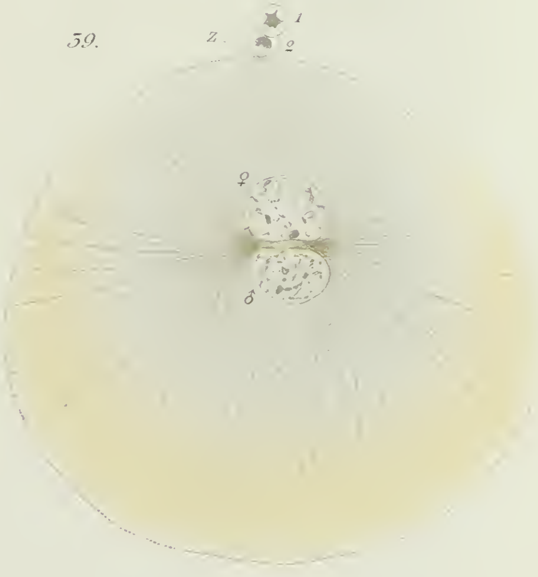

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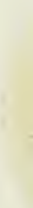

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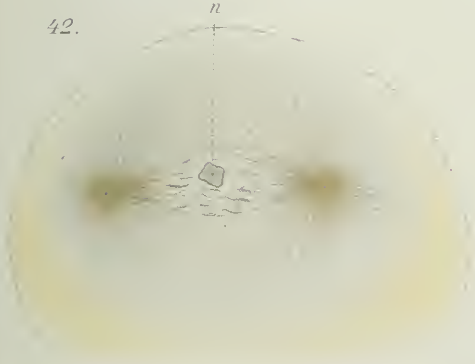

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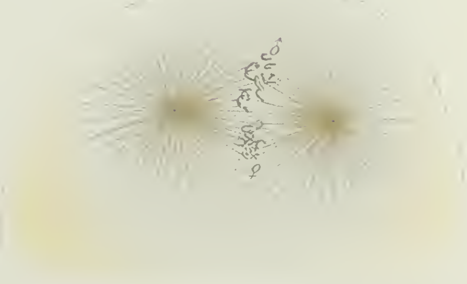

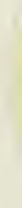

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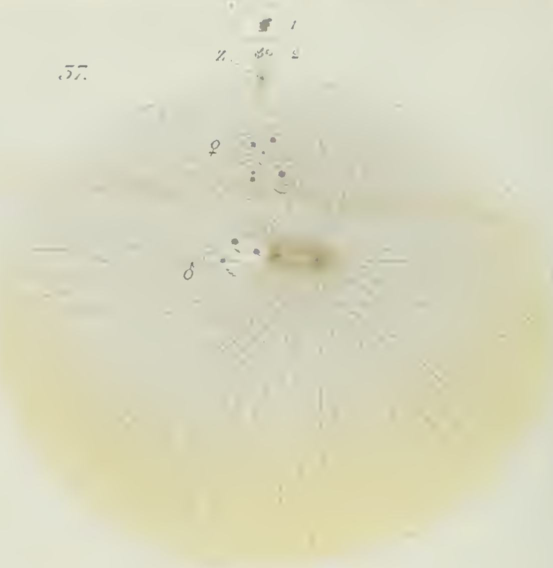

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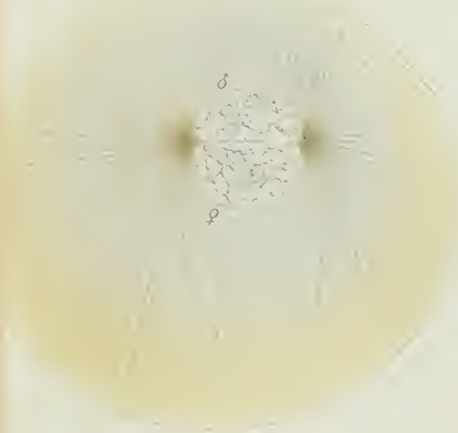

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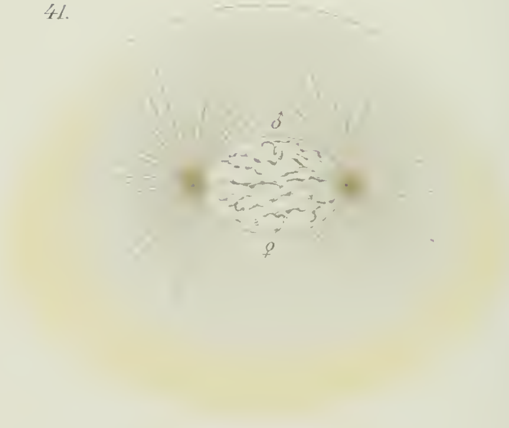

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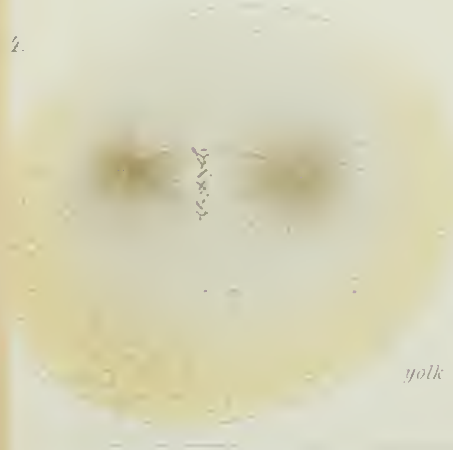

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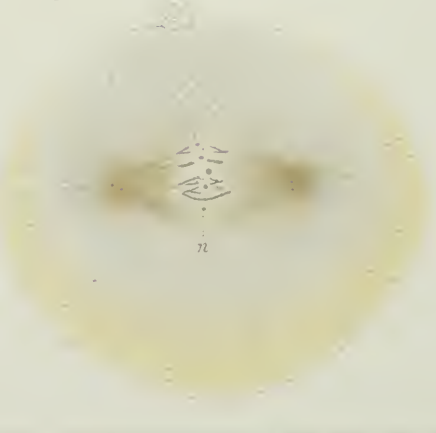

EXPLANATION OF PLATE XIX.

Fig. 46. First cleavage-spindle in the metaphase. Chromosomes moving towards the poles, with nucleoli left in the middle between them. Centrospheres at the height of their development.

Fig. 46a. Late anaphase. The centrosphere at left shows the destructive action of corrosive-acetic acid.

Fig. 47. Two adjacent sections combined. One shows the centrosphere and two brown-black centrosomes with central spindle between them; the other, the eighteen chromosomes, black, belonging to the larger aster. The smaller aster showed the same features.

Fig. 48. First cleavage-spindle in the beginning of telophase; chromosomes commencing to swell up into vesicles. Nucleoli, *n.*, centrospheres, and centrosomes as in the two previous figures.

Fig. 49. Spindle in the telophase; chromosomes vesiculated; fibres in the middle of spindle very distinctly varicose and bent; nucleoli in the midst of spindle. Centrospheres completely resolved so that the rays diverge from the centrosomes directly and are again very extensive, many of them reaching the periphery of the egg. Yolk-lobe, *y.l.*

Fig. 50. Transverse section through the larger cell a little later than the preceding figure. Yolk-lobe, *y.l.* Two adjacent sections combined as in Fig. 47. The two centrosomes with central spindle between them. Eighteen chromatic vesicles.

Fig. 51. Reconstitution of the nuclei. Only one of the two centrosomes in either cell is visible in this section. Middle-plate, *z.*, in many pieces from each of which diverging fibres extend to the nuclei. Nucleoli or first cleavage-nucleus remaining in larger cell, *n.*

Fig. 52. Three consecutive sections, 1, 2, 3, combined: *z.*, *Zwischenkörper*; *n.*, nucleoli of first cleavage-nucleus; $n.^1$, nucleoli in new nucleus. Both centrosomes visible in either cell.

Fig. 53. Smaller of the two cells with resting nucleus. Two asters on opposite sides of nucleus; centrosomes, centrospheres, and comparatively short rays.

Fig. 54. Transverse section of one of the two cells. Nuclear membrane breaking down. Cytoplasmic network; nuclear network; chromosomes, *ch.*; nucleolus, *n.*; two centrosomes and central spindle.

Fig. 55. Transverse section of one of the two cells. Prophase of the second cleavage-spindle; chromosomes, *ch.*; nucleolus *n.*

Fig. 56. Beginning of the metaphase, 2-cell stage. Chromosomes in both centrospheres dividing.

Fig. 57. Transverse section of the smaller of the two cells. Chromosomes undergoing heterotype splitting; centrosomes distinctly separate.

Fig. 58. Transverse section of the larger cell of the same egg as Fig. 57. Spindles slightly further advanced. Centrosomes at a considerable distance apart in both asters.

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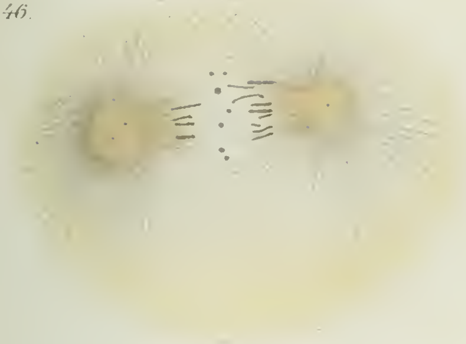

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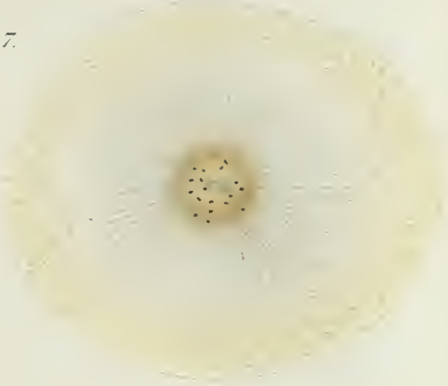

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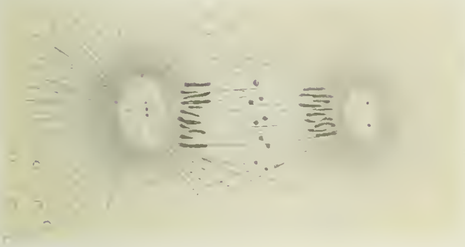

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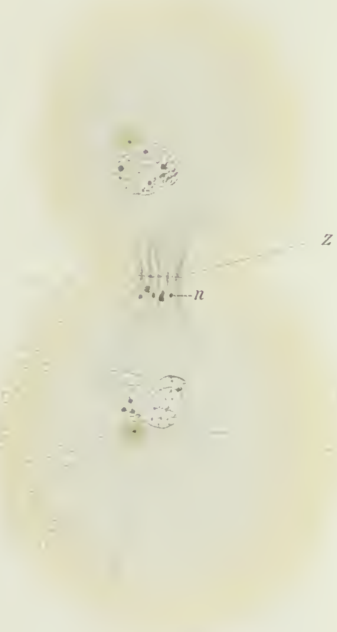

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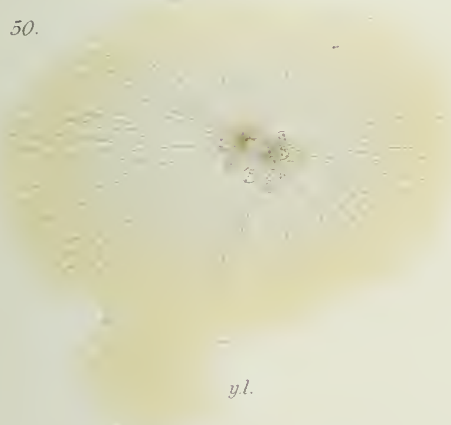

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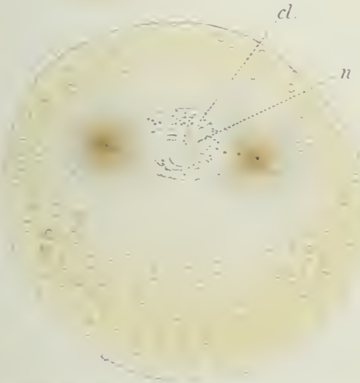

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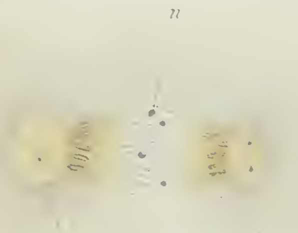

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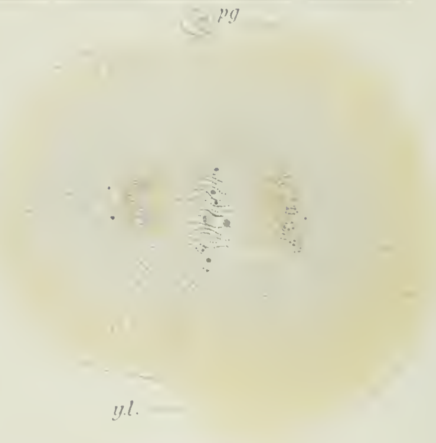

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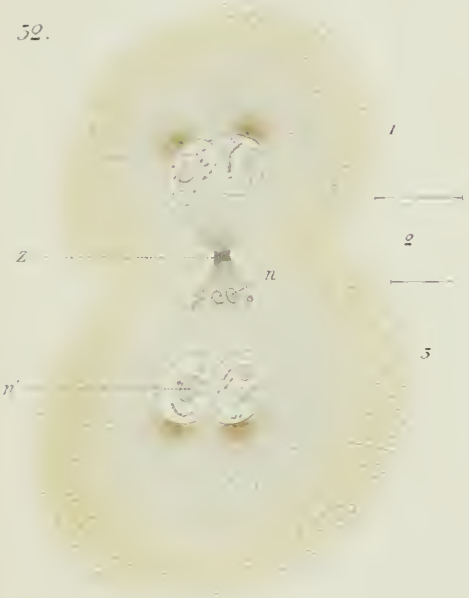

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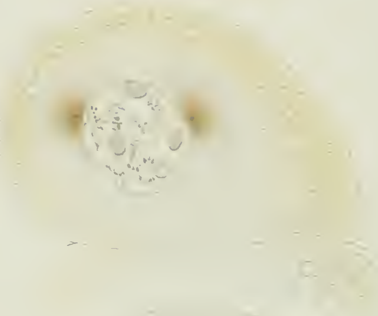

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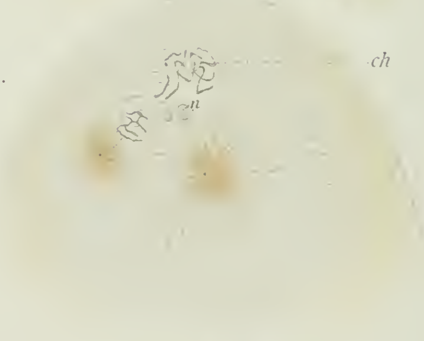

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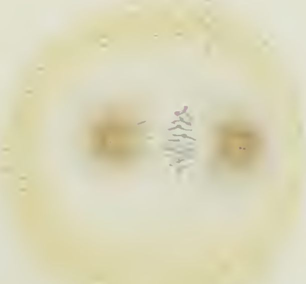

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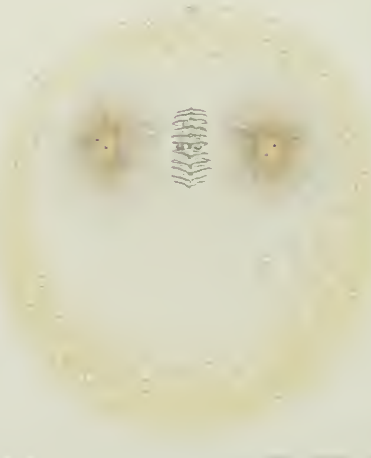

THE RATE OF CELL-DIVISION AND THE FUNCTION OF THE CENTROSOME.

By A. D. MEAD.

Biological Lectures of the Marine Biological Laboratory for 1896-97.

NINTH LECTURE.

THE RATE OF CELL-DIVISION AND THE FUNCTION OF THE CENTROSOME.

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Brown University, Providence, R. I.

There are few phenomena that bring us so close to the fundamental problems of organic development as do those which relate to the origin of the egg and the spermatozoön, to the union of these cells in fertilization, and to the early divisions of the fertilized egg-cell. The egg and the spermatozoön represent the manifold qualities of two separate individuals, and by their union a new individuality is established. In the form and arrangement of the cells into which this oösperm divides, we can recognize the rudiments of the adult body often before the cells become too numerous to be counted; indeed, in many animals the early cleavage-cells constitute a free swimming larva of specific form and possessed of definite functional cellular organs, before the constituent cells are seventy in number, and within four or five hours after the egg is fertilized.

When the organism is composed of so few cells, it is obvious that the specific form of the body, — the size and relations of its organs, — is directly dependent upon the size of every component cell in comparison with the others, upon the position which the several cells occupy in the whole aggregation, and upon the number of cells which perform the same function and constitute a particular organ. The cells which compose the body at a later period of development are but the lineal descendants of those which compose the early larva, and the conclusion follows that the form of the body at any period of development is a resultant of (*a*) the *relative size of the cells* which constitute the several parts, (*b*) the *direction of the cleavage* to which the cells owe their position, and (*c*) the *rate of cleavage* of the various blastomeres, *i.e.*, the intervals of time between successive divisions, by which the number of cells in any part is determined. If we could discover the factors which determine respectively these three component features of development, we should have material for an explanation of the origin of the specific form of the animal body, embryonic or adult.

The problems relating to the rate of cleavage and the size of the resulting cells have received much attention from various investigators, and we will limit ourselves for the present to a consideration of the third factor — *the rate of cleavage*. The effect of the rate of cell-division in determining the form of the embryo is well shown in the early stages, especially in those forms in which the cleavage is "constant and determinate." When the blastomeres in one part divide faster than those in another, important changes take place in the form of the embryo. The "teloblasts" in Clepsine, Rhynchelmis, and Lumbricus, for example, early give rise by their rapid divisions to the germ-bands of the nerve-cords, nephridia, muscles, and other portions of the ventral plate of the trunk, while the divisions of the cells near the apical pole are less rapid, and this region changes more slowly. If the form of the embryo is affected by the differences in the rate of cell-division in certain regions, our problem is to find out the factors which account for these differences. In seeking them, let us first examine the cell-division in the early stages of the embryo, and afterwards those which occur later in the life-cycle.

The "cleavage stages" in certain annelids and mollusks are especially favorable for our purpose, because the behavior of particular cells can be followed with precision, the cells being few and their manner of division constant. In the annelid Amphitrite, up to about the 64-cell stage, the differences in the rate of division among the various blastomeres are comparatively slight, so that all sixty-four cells belong to the same generation

(Fig. 1). In the subsequent cleavages, however, the differences are very pronounced, and the cells may be classed in four categories, according to their peculiarities with reference to the rate of division: (1) cells which divide much more rapidly than any of the others, *e.g.*, those marked *x* and *m* in the diagram, which form respectively the ectoderm and the mesoderm of the trunk; (2) cells which divide more slowly but continuously, *e.g.*, *ec*, which form part of the general ectoderm of the head; (3) cells which cease dividing for a considerable period, but later resume their karyokinetic activity and undergo rapid segmentation, *e.g.*, the entoderm cells, stippled in the diagram; (4) cells which never divide nor show any signs of karyokinetic activity, *e.g.*, those marked *p*, and these soon develop motile cilia and constitute the primary prototroch,—a larval organ of locomotion. In the latter category may be placed also the cells marked *p′*, for three of the four cells derived from the division of each of these also cease dividing, become ciliated, and contribute to the formation of the prototroch.

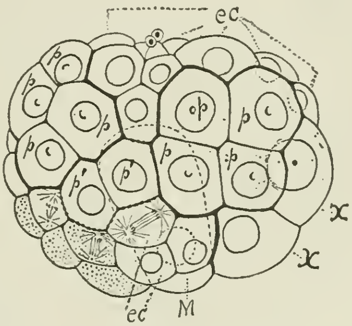

FIG. 1.—Side view of the egg of Amphitrite at about the 64-cell stage. The heavy lines indicate areas of differentiation; *p*, primary prototroch-cells; *p′*, secondary prototroch-cells; *x*, somatic plate; *ec*, general ectoderm; *m*, mesoderm; stippled cells, entoderm.

What are the influences which compel the prototroch cells (*p*) to cease dividing, while the adjacent cells (*x*) divide with extraordinary rapidity? Why do the cells of the general ectoderm (*ec*) divide at an ordinary rate, while karyokinesis in the neighboring entoderm cells is temporarily suspended?

Many more or less plausible suggestions as to the nature of the extrinsic conditions which determine the behavior of cleavage cells have been advanced by students of developmental mechanics, the gist of which is tersely expressed by Driesch: *The prospective significance of a blastomere is a function of its position*, the effects of mutual pressure, of surface tension, of gravity, etc., varying according to the position of the blastomeres in the egg, and according to the position of the egg itself.

That the environment of a cell due to its *position* in the egg does not account for its rate of cleavage in the egg of Amphitrite would appear from the following: (1) adjacent cells may have entirely different rates of cleavage, the one dividing not at all, the other dividing rapidly; (2) cells which occupy exactly corresponding positions in different quadrants of the egg exhibit great diversity in the rate of cleavage; (3) the power of dividing is *suddenly* lost in the cells which form the prototroch — there is not a gradual waning of karyokinetic activity in the successive generations preceding these particular blastomeres; (4) the rate of division in the various cells is the same in whatever position the egg may lie.

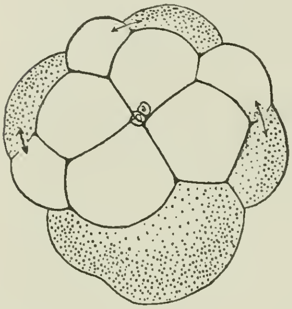
FIG. 2. — Egg of Scolecolepis from above. The four cells at the animal pole undivided; the yolk-laden cells at vegetative pole undergoing division.

Moreover, in related eggs of the same cleavage type, certain blastomeres have a very different environment by virtue of the difference in the absolute and in the relative size of their neighbors, but the rate of cleavage does not vary accordingly. Thus, the cells which form the prototroch in Amphitrite, Clymenella, and Arenicola, respectively, are different in their absolute and in their relative size; yet the cessation of division occurs at exactly the same period of cell development in all three annelids.

Balfour's generalization that the divisions occur more frequently or less frequently according as the cells contain little or much yolk in proportion to the protoplasm has been shown by many observers to be of only limited application. One of the annelids well illustrates the inadequacy of this "law." In the 8-cell stage of Scolecolepis the four lower blastomeres contain all the yolk of the egg and are many times larger than the four upper blastomeres, which are free from yolk; and yet the four yolk-laden cells divide sooner than those which contain only pure protoplasm (Fig. 2).

The same differences in the rate of division that exist in the early cleavage of the ovum obtain in the later stages of the life-cycle. The cells constituting the Malpighian layer of the epidermis in vertebrates and the apical "budding zone" in certain annelids continue to divide throughout life. Other cells, in which for a long time karyokinetic activity is suspended, may upon occasion undergo rapid division; *e.g.*, the cells which give rise to the temporary ovaries in some of the lower invertebrates and the cells which commence the regeneration of lost tissues. Many cells also, *e.g.*, the neuroblasts, cease dividing permanently.

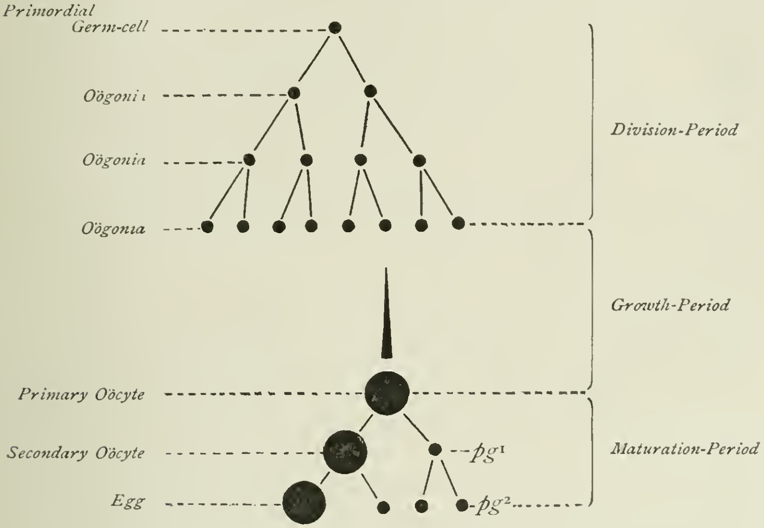

Fig. 3. — Diagram showing the development of the mature egg from the primordial germ-cell (after Boveri).

I wish, however, particularly to call attention to the peculiarities in the rate of cell-division exhibited towards the close of the life-cycle by the cells which give rise to the mature ovum. After a long series of consecutive divisions of the oögonia (Fig. 3), a generation of cells arises in which karyokinesis is, for a time, suspended. These cells are the *un*maturated eggs — the "*primary oöcytes*." The oöcyte, after enjoying a period of rest and growth (which may sometimes be measured in months or even in years), sooner or later divides into a small cell — the first polar globule, and a large cell — the *secondary oöcyte*. The latter also divides to form a small cell —

second polar globule, and a large cell — the mature egg. With this division the life-cycle is completed, the mature egg representing the last generation of cells.

Beginning with the formation of the primary oöcyte, the phenomena of cell-division recall those in the cleavage stages of Amphitrite. In the oöcyte, as in the cleavage-blastomeres, we meet with cells which cease to divide temporarily and with others of a definite generation which, left to themselves, never divide. The peculiarities in the rate of division of the oöcytes are rendered more significant by the fact that in almost all known cases, in both animals and plants, the same phenomena obtain, *viz.*, that not more than two successive divisions of the primary oöcyte take place (unless fertilization occurs to initiate a new cycle of division) before there is a permanent cessation of mitosis.

It is now pertinent to ask, *What are the factors which determine the rate or time of division of the oöcytes, and why does the maturated egg cease dividing until fertilization takes place?* That the behavior of the oöcytes is not a "function of their position" is evident from the enormous differences in the physical surroundings of various eggs at this period. Is there any known structure *within the cell* by whose activity the division may be incited and in whose absence the cell cannot divide? Boveri's theory of the *centrosome*, which has been endorsed by a large number of eminent workers, gives an affirmative answer to this question. According to this theory, the centrosome is necessarily present in mitosis; the attraction sphere, astral rays, and spindle fibers of the mitotic figure arise under its influence. The centrosome is, in fact, the special organ of cell-division, — "the active centre of cell-division in the cell-body."

It is interesting that a large part of the evidence in support of this theory has been drawn from the behavior of the centrosome in the maturated ovum, the cell now under discussion. According to Boveri, this cell is unable to divide because it has lost its centrosome through degeneration. It may resume karyokinetic activity only when a new centrosome is brought in by the entering sperm. "The ripe egg possesses all of the organs and qualities necessary for division excepting the centrosome, by which division is initiated. The spermatozoön, on the other hand, is provided with a centrosome, but lacks the substance in which this organ of division may exert its activity. Through the union of the two cells in fertilization all the essential organs necessary for division are brought together ; the egg now contains a centrosome which by its own division leads the way in the embryonic development." "It is the centrosome alone that causes the division of the egg."[1]

The behavior of the centrosome in fertilization, as recorded by many recent observers, *may* be interpreted as a substantiation of Boveri's conclusions, for the centrosomes which are demonstrable in the egg during those divisions which result in the formation of the two polar globules totally disappear, and the centrosomes which participate in the first cleavage mitosis arise at any rate *near* the sperm-nucleus, and, moreover, in many instances are actually brought into the egg by the spermatozoön (Boveri, Wilson, Matthews, Hill, Fick, Henking, Kostanecki, and Wierzejski, Rückert, and others). In parthenogenetic eggs, where no spermatozoön enters, the centrosomes ought, according to Boveri's theory, to remain and to organize the machinery for the first cleavage mitosis. Brauer has shown that the parthenogenetic egg of Artemia fulfills the requirements of this theory, for the egg centrosomes actually remain and form the cleavage amphiaster.

These observations furnish ground for the belief that the egg-cells cease dividing, because they lack the active agent in cell-division, — the centrosome. The loss of this organ has been regarded as a "provision to guard against parthenogenesis." Thus, according to this interpretation, the rate of cell-division in the cells of at least one generation is conditioned upon the presence of the centrosome.

Since the essential features of mitotic division are the same throughout the life-cycle, it would seem probable, *a priori*, that the factors which inhibit or incite the mitotic activity of the egg-cells would also determine whether the cells of other generations should or should not divide. Or, to be more explicit, if the division of the mature egg-cell is inhibited because its centrosome degenerates, and is subsequently resumed because a new centrosome is introduced, it is fair to infer that the division of a blastomere, a tissue-cell, or an *oöcyte* is also conditioned upon the presence of the centrosome. For example, the prototroch-cells in the annelid larva, or the neuroblasts in the vertebrate embryo, cease to divide because the "centrosomes by which division is initiated" have degenerated. Again, the cells by whose rapid division lost tissues are regenerated resume their mitotic activity upon the acquisition of a centrosome.

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[1] Boveri, Wilson "Cell."

With this explanation in mind, let us return to a more critical examination of the phenomena of mitosis in the germ-cells at the close of the life-cycle; *viz.*, to the division of the primary and the secondary oöcytes and the mature egg.

It is noticeable, in the first place, that among different species of animals the mitosis is not always suspended in the same generation of cells. Accordingly, the eggs of the various species may be arranged in five classes: first, those in which the primary oöcyte remains with germinal vesicle intact until the sperm enters (for example, Thalassema, Nereis, Fig. 4, *A*); second, those which, if deposited in sea-water, remain with the first maturation amphiaster in the metaphase (for example, the annelid Chaetopterus, Fig. 4, *B*); third, those in which the secondary oöcyte awaits the spermatozoön (for example, the frog, Axolotl, lamprey, Fig. 4, *C*); fourth, those in which the maturated egg, after the formation of both polar globules, awaits the sperm (for example, the sea-urchin, Fig. 4, *D*); and fifth, those (parthenogenetic eggs) which begin the subsequent cycle of divisions without being fertilized.

Let us grant for the moment that the parthenogenetic egg continues to divide because its centrosomes do not degenerate, and that the fertilized egg of the sea-urchin divides because the entering sperm brings in the centrosomes which organize the machinery of mitotic division. It is difficult to apply the same principle to the eggs of the first, second, and third classes, *i.e.*, to those which do not complete the maturation divisions until the spermatozoön enters, for the amphiasters of the maturation divisions do not involve the sperm-centrosomes, but are separate and independent of them. The first maturation amphiaster in certain eggs, *e.g.*, Thalassema, Nereis, and Myzostoma, is formed only after the sperm enters, and yet its centrosomes are not brought in by the sperm nor do they arise near it. In Chaetopterus, on the other hand, a complete amphiaster with centrosomes, centrospheres, astral rays, and spindle fibers is developed and remains for hours in the metaphase, if the egg is left unfertilized in sea-water; and the same appears to be true of many other marine annelids. This elaborate machinery of mitotic division is immediately set in motion upon the entrance of the spermatozoön, though the sperm and its centrosomes are in a distant portion of the egg. All the phases of this and the subsequent mitosis are independent of the karyokinetic changes in the vicinity of the sperm.

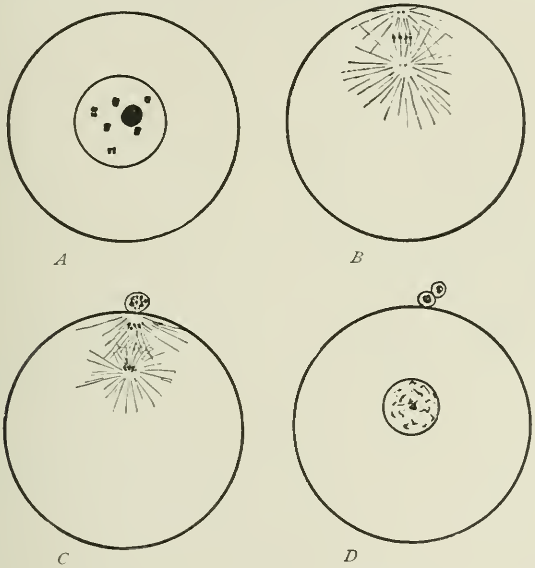

Fig. 4. — Diagram indicating the different stages of maturation attained by the eggs of various animals before the sperm euters. *A*, Nereis, Thalassema; *B*, Chaetopterus and some other marine annelids; *C*, frog, Axolotl, lamprey; *D*, sea-urchin.

Since in one form the oöcyte will not divide until the sperm enters the cell, even though the *centrosomes* and the whole amphiaster *are present*, the suspicion is warranted that in the ripe egg of other forms — the sea-urchin, for example — the mitosis is not inhibited merely on account of the *lack of a centrosome*, nor is it incited merely because a new centrosome is introduced to organize the mitotic figure.

Other observations on fertilization strengthen this supposition. Wheeler has shown in Myzostoma that no centrosomes or asters are developed in connection with the male pronucleus, and that the centrosomes, which are left in the egg after the formation of the polar globules, probably form the poles of the cleavage-spindle. According to Lillie, the sperm-centrosomes in the egg of Unio degenerate, and the centrosomes which participate in the first cleavage mitosis are egg-derivatives. The well-known researches of Fol, Guignard, and Conklin, even if they are not complete enough to prove the theory of the "quadrille," certainly indicate that the egg-centrosomes have a considerable degree of persistence.

Furthermore, it is difficult to demonstrate that the "sperm-centrosomes" are actually brought into the egg by the spermatozoön, and caution must be exercised in referring the origin of the sperm-centrosomes to this source.

Just how the entrance of the sperm revives the latent activity of the oöcyte is not yet fully understood, but the phenomenon is suggestive in that it shows that it is neither the mass of the cell, nor the abundance of yolk, nor the position of the cell, nor the presence of the centrosome that determines the time or rate of cell-division, but that a *stimulus* is required analogous, perhaps, to that which starts into activity the motor apparatus of pigment-cells, leucocytes, or muscle-cells. Following out this suggestion, I have made some experiments upon the unfertilized egg of Chaetopterus.[1]

Watasé has pointed out that the "mechanism of protoplasmic motion" in the leucocyte, pigment-cell, and muscle-cell is similar in its essential features to that in a blastomere during mitotic division (Fig. 5). The aster in the leucocyte and the fibrils, contraction-bands, etc., in the muscle-cell are, most of them, permanent features of these cells, persisting even when the cells are at rest. In the dividing cell the corresponding structures are, as a rule, only transitory. The primary oöcyte of Chaetopterus, however, is a remarkable exception to the rule. So long as the oöcyte remains in the body-cavity of the worm, it contains a large germinal vesicle and no trace of asters or centrosomes; but, after it has been deposited in sea-water, a typical amphiaster with distinct centrosomes at either pole is developed. If the egg is not fertilized, the amphiaster on reaching the metaphase (Fig. 4, *B*) remains in this stage for hours, resembling in persistence, as well as in structure, the motor apparatus of leucocytes and muscle-cells.

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[1] I am glad to acknowledge the valuable suggestions and kind assistance of my friend, Mr. C. W. Green, of Johns Hopkins University.

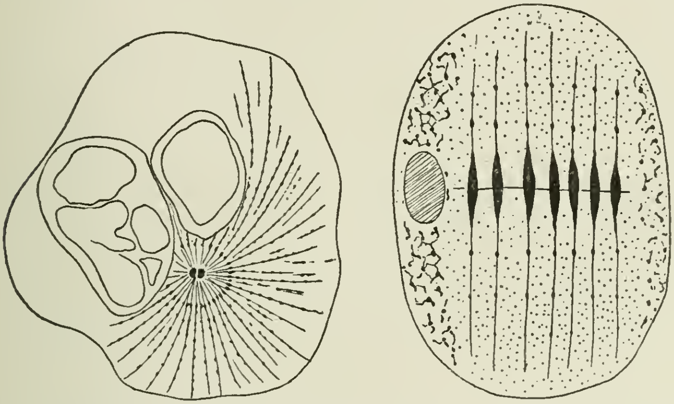

FIG. 5. — Diagram of the motor apparatus in the leucocyte and in the muscle-cell (after Watasé).

The leucocyte, as is well known, is susceptible to chemotactic influences; certain chemical substances, *e.g.*, those elaborated by bacteria, will stimulate the motor mechanism of this cell to *normal* activity. Likewise, as Mr. Green has proved, isolated portions of the turtle's heart will resume the normal rhythmical contractions upon the introduction of extremely weak solutions of certain salts; *e.g.*, sodium, calcium, potassium and magnesium. May not the analogous mechanism within the oöcyte of Chaetopterus be induced to resume its normal activity upon the introduction of a similar stimulating substance?

If this oöcyte, in which the maturation spindle has been developed, is placed in a solution of from ¼% to ½% KCl in sea-water, *the normal mitotic activity is immediately resumed.* The maturation processes, including the extrusion of the first and second polar globules and the concomitant changes in the form of the egg, succeed one another with the same regularity that obtains when the egg is fertilized. In both instances the egg, at first spherical, becomes flattened at the animal pole just before the first polar globule is formed, but soon regains its original form. About the time the second polar globule is formed, the contour again changes and the egg becomes pear-shaped, the apex towards the animal pole. After this the egg again assumes the form of a sphere (Fig. 6).

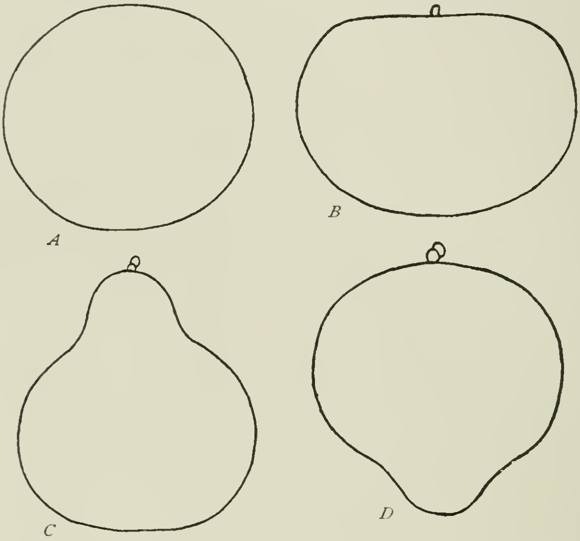

Fig. 6. — Diagram showing some of the changes in the form of the oöcyte and egg-cell which take place upon the entrance of the spermatozoön or upon the addition of potassium chloride to the sea-water. *A*, primary oöcyte before the first polar globule is formed; *B*, secondary oöcyte flattened at the animal pole, first polar globule; *C*, shape assumed when the second polar globule is formed; *D*, formation of the yolk-lobe. (These form-changes are not so pronounced in eggs taken from animals which have been removed from their tubes and have been kept for a few days in an aquarium.)

But the similarity between the behavior of the fertilized eggs and those subjected to potassium chloride does not stop here, for the "yolk-lobe," a protuberance at the vegetative pole, is formed in both in essentially the same manner. In the fertilized egg, however, the first cleavage-furrow cuts the egg into two blastomeres, while the lobe is developing, and the latter is borne upon the larger of the two cells, into which it is afterwards resorbed. On the other hand, in the unfertilized egg stimulated by the salt, the lobe, though it is formed in exactly the same manner, is resorbed into the undivided egg, which then once more resumes the form of a sphere. Occasionally a furrow cuts deeply into the egg at the animal pole and then vanishes again, and eggs are found which have every appearance of being in the 2-cell stage.

In regard to the effect produced by the potassium chloride, I wish to emphasize two points: first, it is of the nature of a stimulus, compatible with the continuance of the normal developmental processes, and is not of the nature of a poison or an irritant setting up irregular, abnormal, and inconstant changes; second, the stimulus must be referred to the specific properties of the salt and not to a change in the density of the water in which the eggs are placed. (1) If the unfertilized eggs are allowed to remain in the potassium chloride solution for only a few minutes and are then returned to normal sea-water, the effect is the same as though they were left permanently in the salt solution. Furthermore, eggs may be fertilized in the potassium chloride solution and reared to free-swimming trochophores without being returned to the normal sea-water. (2) If sodium chloride is added to the sea-water instead of potassium chloride, no apparent effect is produced upon the oöcyte; but, if the potassium is added to this solution, or, if spermatozoa be introduced, the polar globules will be formed in the usual manner. Similarly, if the sea-water is diluted by the addition of ⅓ volume distilled water, no effect is produced; but, when the usual amount of potassium chloride is added, the mitosis is immediately resumed.

The behavior of the unfertilized eggs that have been stimulated by the salt is interesting in that it shows how many of the cytokinetic and karyokinetic changes, which are initiated by the entrance of the sperm, are independent of the sperm-nucleus, "sperm-centrosomes," and asters. In the fertilized egg, while the polar globules are being formed, asters are developed about the sperm-centrosomes. These asters grow continuously and a spindle develops between them, so that by the end of the maturation-period the egg contains a huge amphiaster with extensive rays. The recession of the egg-nucleus appears to be influenced by the presence of this amphiaster and the sperm-nucleus. The development of the yolk-lobe would seem almost certainly to be correlated with the development of the cleavage-amphiaster, since the various phases in its growth and resorption correspond with the definite phases of the cleavage mitosis. Nevertheless, in the unfertilized eggs stimulated with potassium chloride the two maturation-divisions, the reconstitution of the egg-nucleus and its inward migration, and even the protrusion and resorption of the yolk-lobe, take place in the constant and orderly sequence which is characteristic of the fertilized eggs, though there is nothing in them corresponding to the sperm-nucleus or sperm-centres. In the one case, when the yolk-lobe is formed, the egg contains an enormous amphiaster; in the other, no amphiaster or radiations are present.

Although the unfertilized egg will remain in the normal sea-water for several hours without apparent change of form and without loss of the capacity for maturation and fertilization yet, if it is stimulated with potassium chloride, not only do the phenomena of maturation ensue, but, after about an hour and a half, the egg begins to break up into more or less irregular segments, which frequently resemble the ordinary cleavage-blastomeres. The karyokinetic activity *sensu strictu* does not stop with the reconstitution of the egg-nucleus; but, though the sperm-nucleus, amphiaster, and centrosomes are absent, the nine constituent chromosomes divide and the daughter-chromosomes swell up into vesicles which usually remain in one cluster or are irregularly scattered about, and resemble those found in the telophase of ordinary mitosis. At this stage, however, the egg is no longer devoid of radiations. On the contrary, an enormous system of fibers radiates from the centrosphere, which surrounds the group of vesicles and extends in all directions to the periphery. The rays have the appearance characteristic of normal mitosis when the chromatic vesicles have reached this particular stage of development. Not infrequently, when by virtue of a favorable distribution of the chromosomes these cytoplasmic rays converge towards one point, a dark body — centrosome — may be seen at the point of convergence.

These experiments show that a chemical stimulus, applied for a short time to the oöcyte in Chaetopterus, initiates a series of mitotic changes which extends over a much longer period. The maturation-divisions, reconstitution of the egg-nucleus, and extrusion of the yolk-lobe occur exactly as though the sperm had entered the egg. It is a natural inference from these phenomena that, in normal fertilization, the entering sperm stimulates these mitotic activities in a similar manner, *i.e.*, by exerting a chemical influence upon the egg and not by furnishing the egg with special organs of division. Indeed, the cytokinetic changes, including the formation of the centrosome, seem rather to be in response to the activity of the nucleus than *vice versa*.

This is the more plausible interpretation of those cases in which the entering sperm initiates mitotic division without the participation of the "sperm-centres." According to Wheeler, no middle-piece or centrosome can be distinguished in the sperm of Myzostoma, though the latter initiates the normal mitosis in the egg exactly as it does in Chaetopterus. Moreover, even in the egg of the sea-urchin, Richard Hertwig has shown that strychnine stimulates the production of asters and even of an amphiaster, although he finds no centrosome.

In the egg of Chaetopterus, which has been stimulated by potassium chloride, two consecutive mitoses are completed in the normal fashion, and the abnormal phenomena commence only after the reconstitution of the egg-nucleus. The abnormalities may, perhaps, be referred to the lack of sperm-chromosomes, which are necessary to complete the full number in the cell. That the full number of chromosomes is essential to normal cell activity is attested by its constancy in all tissue-cells and by the universal occurrence of "reduction" before fertilization. The continuance of the cell-divisions in the parthenogenetic eggs of Artemia is also, perhaps, due to the fact that the chromosomes of the second polar globule remain in the egg, rather than to the fact that the centrosomes persist.

From our new point of view we may briefly reëxamine the rate of cell-division in the cleavage-blastomeres.

Let us take, in the first place, as a specific example, one of the prototroch-cells of Amphitrite (Diagram I). It would be difficult to maintain that this cell is unable to divide because of the absence of a vigorous centrosome, inasmuch as it must inherit this structure as an heirloom from the previous cells in whose mitosis there was no indication of waning activity. The inhibition of the division of the prototroch-cell would seem not to depend upon its position, nor upon the absence of an organ of division, but upon the metabolic activity peculiar to the cell by virtue of its internal structure.

The blastomeres adjacent to the prototroch-cells have a different structure, and consequently a different metabolic activity, one expression of which is a difference in their rate of cleavage.

We would not imply that the rate of cleavage of the blastomeres is unaffected by stimuli from without the cell, coming from intercellular secretions, from the medium in which the egg lies, or from some other source; indeed, the effect of potassium chloride upon the oöcyte and egg-cell is evidence to the contrary. The position occupied by one blastomere may be more favorable for the reception of these stimuli than that occupied by another; yet the extreme differences in the rate of division exhibited by cells which are adjacent in time or in space are out of all proportion to the differences in their positions.

The peculiar organization of the cell determines the character of its response to a stimulus — determines whether the cell shall or shall not divide.

THE CELL ORIGIN OF THE PROTOTROCH.

By A. D. MEAD.

Biological Lectures of the Marine Biological Laboratory for 1898.

SIXTH LECTURE.

THE CELL ORIGIN OF THE PROTOTROCH.

A. D. MEAD,

BROWN UNIVERSITY.

NOTWITHSTANDING the wholesome reaction against the frequently reckless application of Baer's biogenetic law, larval and embryonic characters still hold an important place as criteria of the relationship of organic forms. The larval characters of the tunicates are significant indices of the relationship of these animals to the vertebrates, but perhaps no larval form has rivalled the trochophore or trochosphere in provoking phylogenetic speculation. The splendid work of Roule, *L'Anatomie Comparée*, which has appeared within the last year, bears witness to the importance which is at present attached to this larval type in establishing the relationship of such various forms as the annelids, rotifers, bryozoans, mollusks, etc. All these forms are grouped together by him into one branch of the animal kingdom, the *Trochozoa;* for, although the bodies of the different *Trochozoa* are highly variable in form and structure, they all may be derived in the normal embryonic development from the trochophore larva, which is constructed on one constant organic plan.

The features characteristic of the trochophore arise in various *Trochozoa* under very different conditions of embryonic development, and are possessed by some adult animals, for example, *Trochosphæra* (Semper). These facts give deep interest and wide bearing to the comparative study of the embryonic origin of the trochophore itself.

One of the essential structural characters of this larval form is the transverse ciliated fringe, *the prototroch* (Figs. 13–16), and it is the purpose of this paper to bring together and compare the observations of several workers who have employed the method of cell-lineage to determine the exact origin of this organ.

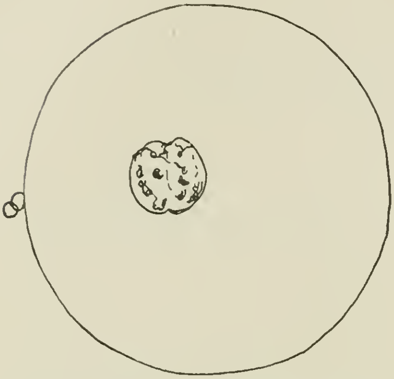

Fig. 1. — Left side of fertilized unsegmented egg of *Amphitrite*. Polar globules indicate the position of the animal pole.

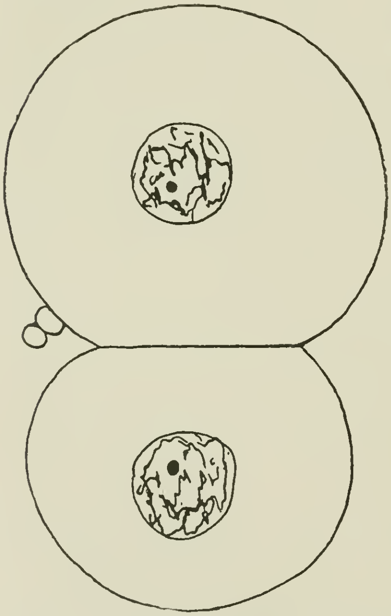

Fig. 2. — Left side of *Amphitrite* egg, 2-cell stage, oriented as in Fig. 1.

In order to establish a concrete example for comparison, let us proceed at once to the account of the origin of a simple and fairly typical prototroch, namely, that of the marine annelid *Amphitrite*.

The spherical egg is of medium size, about one-tenth of a millimeter in diameter, without much yolk, and is unprotected save by a thin wrinkled egg membrane. Fig. 1 represents the egg seen from the left side. Fertilization has taken place, and the polar globules remain attached. The succeeding figures represent the egg in the same position, unless otherwise stated. Fertilization takes place in the sea water, and the cleavage progresses so rapidly that the larva swims in a few hours. The first cleavage being unequal, the 2-cell stage is characterized by the possession of a larger and a smaller blastomere, which are represented in side view in Fig. 2. After this the cells divide with some irregularity in time and in the size of the resulting blastomeres, yet the irregularity is not so great as to obscure the rhythm of cleavage, which expresses itself in the following manner:

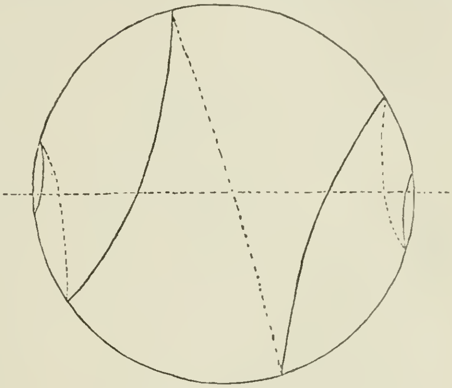

FIG. 3. — Loxodromic curve ("left-handed spiral") described about a sphere, showing the general direction of the cleavage furrows which cut the cells of the 2-, 8-, and 32-cell stages.

Each of the two cells divides, so that we have a 4-cell stage; then each of these cells divides, and so on, the number of cells increasing in geometrical progression until the egg consists of sixty-four cells. A distinct rhythm is observed also in the direction of cleavage, for the cleavage planes lie obliquely across the meridians of the egg. The cells in the 2-, 8-, and 32-cell stages are divided by cleavage furrows which take the general direction of the loxodromic curve in Fig. 3,[1] which may be rather loosely but conveniently defined as a left-handed spiral described around a sphere from pole to pole. The cells of alternate generations, namely, of the 4- and 16-cell stages, are cut by furrows which have an opposite direction, as represented in Fig. 4. These curves may be called, for convenience, left and right respectively, following the conventional nomenclature for the threads on a screw.

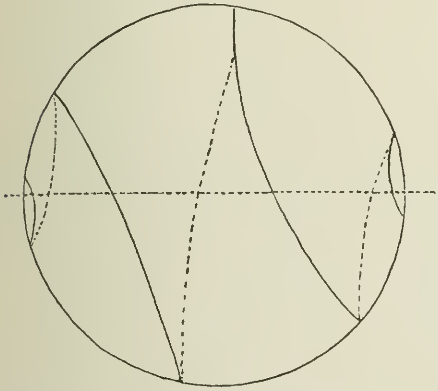

FIG. 4. — Loxodromic curve ("right-handed spiral"), having the general direction of the furrows which cut the 4- and 16-cell stages and many of those of the 64-cell stage.

The rhythm of division

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[1] In the diagram this curve cuts the equator at one point only. The curve will, of course, cut the equator at any point, if rotated.

ceases abruptly at the 64-cell stage. The cells of this stage are, of course, all of the same generation, the seventh, counting the ovum as one; yet, as a consequence of the obliquity of the cleavage furrows, the cells are not directly superimposed, but alternate with one another.

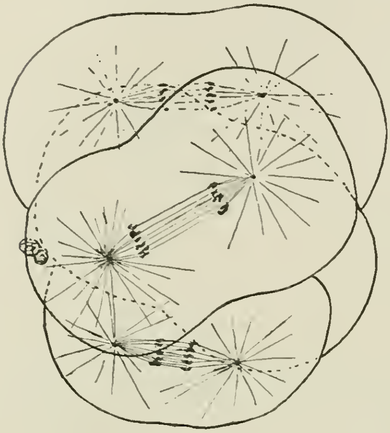

Fig. 5. — *Amphitrite*, left side, four cells getting ready to divide into eight.

For many reasons it is helpful to conceive of the egg as consisting of four quadrants, each of which is composed of the derivatives of one of the cells of the 4-cell stage. Any cell in one quadrant corresponds in origin and in position to a cell in each of the other quadrants.

Let us consider the egg in the 4-cell stage (Fig. 5) as composed of one quartette of cells about to divide. Four of the descendants of each of these cells will belong to the *primary* prototroch. In a similar way the egg in the 8-cell stage consists of two quartettes of cells, those of one quadrant meeting at the anterior pole, the position of which is indicated in Fig. 6 by the polar globules, those of the other meeting at the posterior pole. *The primary prototrochal cells are all descended from the cells of the anterior quartette,* and from that portion of the cells which is stippled in Fig. 6. The cells of this quartette, or, in the latter stages their descendants, constitute the anterior *hemisphere,* or *umbrella,* and the cells of the posterior quartette constitute the *posterior hemisphere,* or *subumbrella.* The hemispheres are separated in the drawings by a dotted line.

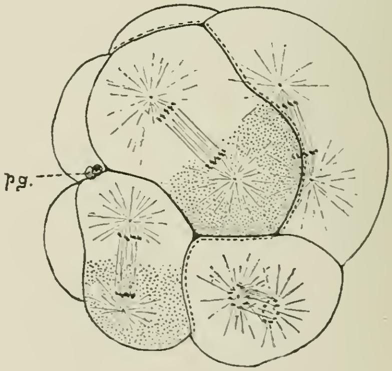

Fig. 6. — *Amphitrite*, left side, last phase of 8-cell stage.

After the next cleavage the 16-cell stage is formed, in which the cells are disposed in four quartettes. Fig. 7 represents the egg in this stage seen from the side, but slightly rolled to show all the eight cells of the anterior hemisphere. The polar globules lie in the middle of the hemisphere. The derivation of the cells from those of the 8-cell stage is indicated by the arrows, and the furrow between each pair of cells has the general direction of the loxodromic curve in Fig. 3. The dotted line indicates the boundary between the two hemispheres, and the heavy lines separate the quadrants. The four cells which are stippled in Fig. 7, one in each quadrant, are the *primary trochoblasts in the strict sense, for they contain all the material of the primary prototroch and no other material.*

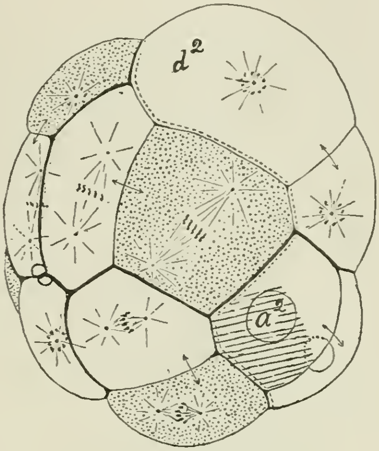

FIG. 7.—*Amphitrite*, from left side and top, 16-cell stage. Heavy solid lines divide the quadrants; dotted lines divide the anterior and posterior hemispheres.

By the division of the sixteen cells represented in Fig. 7 the 32-cell stage is attained (Fig. 8). It consists of eight quartettes (four cells in each quadrant), two of them, the third and fourth, from the animal pole, being derivatives of the primary trochoblast and stippled as in Fig. 7. (Fig. 8 really represents the beginning of the transition between the 32- and 64-cell stage. Two of the cells of the subumbrella hemisphere have divided. These cells, however, do not concern us especially.)

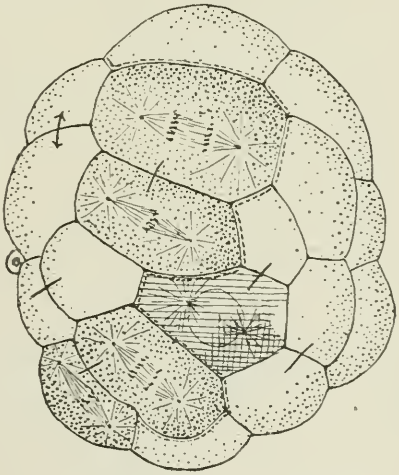

FIG. 8.—*Amphitrite*, left side, 32-cell stage.

The spindles in the trochoblast cells indicate the direction of their next division, which results in the 64-cell stage (Fig. 9). Fig. 10 is an apical view of the anterior hemisphere in the 32-cell stage, showing the four alternating quartettes of umbrella cells, and the uppermost quartette of sub-umbrella cells. The cells of the first quartette have the nuclei figured; those of the second are left clear; those of the third and fourth quartettes (primary trochoblast cells) are stippled. All of the thirty-two cells divide again, so that the egg is composed of sixty-four cells, arranged in sixteen quartettes, making sixteen cells in each quadrant. Four of these quartettes, the fifth, sixth, seventh, and eighth, stippled in Fig. 11, comprise the cells of the *primary prototroch.*

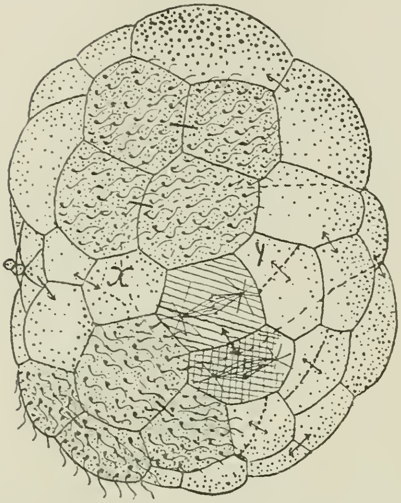

FIG. 9. — *Amphitrite*, 32-cell stage, from anterior end. View of umbrella or anterior hemisphere.

It is obvious that, in consequence of the regularity of cleav-

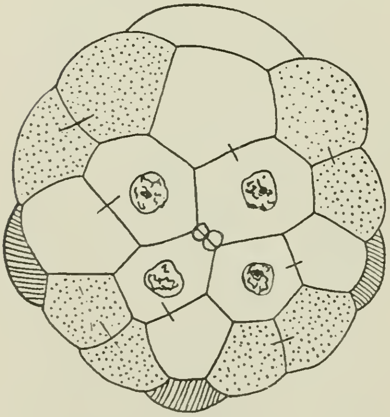

FIG. 10. — *Amphitrite*, from left side. Primary and secondary, shaded, respectively, with dots and lines.

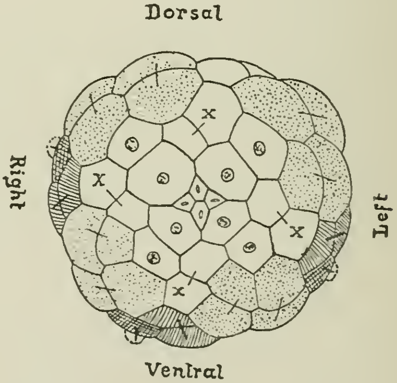

FIG. 11. — *Amphitrite*, beyond 32-cell stage, from anterior poles, slightly distorted to show all 25 prototrochal cells.

age, one-half of all the cells are descendants of the four upper cells of the 8-cell stage (the anterior hemisphere or umbrella), and that the sixteen primary prototroch cells all belong to this hemisphere.

By means of the primary prototroch, which consists of four isolated groups of cells, the egg, or trochophore, as we may now call it, swims about for a considerable time. In the course of a few hours, however, nine more cells, *secondary prototroch*, become differentiated and develop cilia, and these, together with the sixteen cells already described, constitute the *definitive prototroch*. As is shown in Fig. 9, these additional cells, which are shaded with lines, are disposed in such a manner that they fill the spaces between the isolated portions of the primary prototroch except in one quadrant. *Thus the definitive prototroch consists of twenty-five ciliated cells which lie in a nearly complete belt around the trochophore* (Fig. 13, p. 120).

The primary and the secondary prototroch cells, although together they form a single larval organ, have different modes of origin, for the cells of the secondary prototroch are derived from the lower (posterior) quartette in the 8-cell stage, that is, from the posterior hemisphere, or subumbrella.

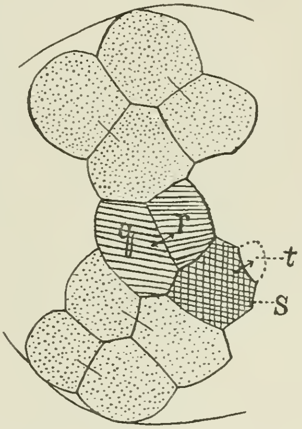

Fig. 12. — Diagram of prototrochal cells, seen from left side, in *Amphitrite*, *Clymenella*, and *Arenicola*. Two groups of primary and one of secondary prototrochal cells.

For convenience of description, we may assume the existence of a specific material which will become the secondary prototroch, and may locate this material in the subumbrella during the successive stages of cleavage. In the 16-cell stage the material occupies a portion of three of the cells of the third quartette, counting from the upper pole, which alternate with the primary trochoblasts. In Fig. 7, p. 117, the cell marked a^2 and partially shaded with lines is one of the three cells in question. The cell marked d^2 belongs to the quadrant which does not contribute any secondary prototroch cells. In the 32-cell stage the material is still in these cells of the highest quartette of the subumbrella. One of them is shown in the side view, Fig. 8, and all three in Fig. 9, shaded with lines. *These three cells may be called secondary trochoblasts, although they contain a small amount of material* (see unshaded portion of cell in Fig. 8) *which does not enter the prototroch.* With the next cleavage each of these cells divides so that the six cells, two in each of the three quadrants, contain the material of the

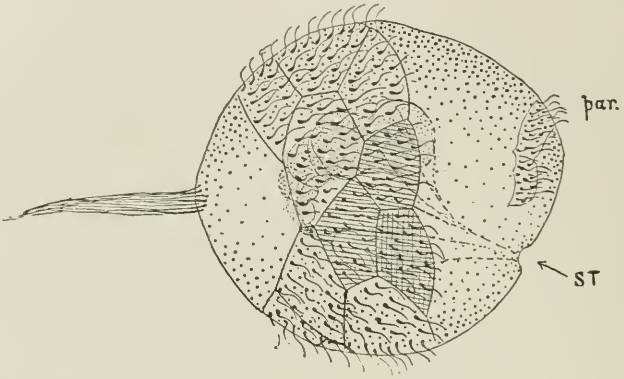

FIG. 13. — *Amphitrite* trochophore, showing apical tuft, prototroch, paratroch, stomadæma, and one arm of mesoblast consisting of six cells.

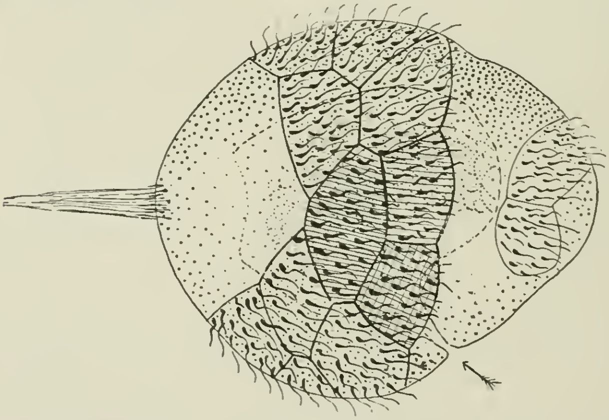

FIG. 14. — *Amphitrite*, left side: prototroch, paratroch: mouth at arrow; outline of archenteron stippled; mesoderm stippled.

secondary prototroch. These finally divide again in the direction indicated by the spindles in Fig. 10. Thus each of the three secondary trochoblasts is at last represented by a group of four cells, *q*, *r*, *s*, and *t*, in Fig. 12. Three of these, *q*, *r*, and *s*, are about equal in size, and constitute the *secondary prototroch.*

The relative position of all the prototroch cells is shown in the apical view of the umbrella hemisphere in Fig. 11, which is slightly distorted and brings the secondary prototroch cells into sight. The shading accords with that of the previous figures. The primary prototroch cells are stippled, the secondary shaded with lines, and the minute products of the secondary trochoblasts are drawn with dotted lines. The unshaded cells in the upper margin between two groups of primary prototrochal cells interrupt the continuity of the prototroch. They correspond in origin, however, to the secondary prototroch cells of the three other quadrants. The remaining cell, *t*, Fig. 12 (dotted in Fig. 11), is small, divides again much later, and has an unknown destiny. The interruption in the continuity of the ciliated band in the mid-dorsal region is later obliterated by the approach and concrescence of the prototroch cells from either side. The completed prototroch, consisting of twenty-five cells, persists for five or six days, until the larva has developed several seta-bearing metameres.

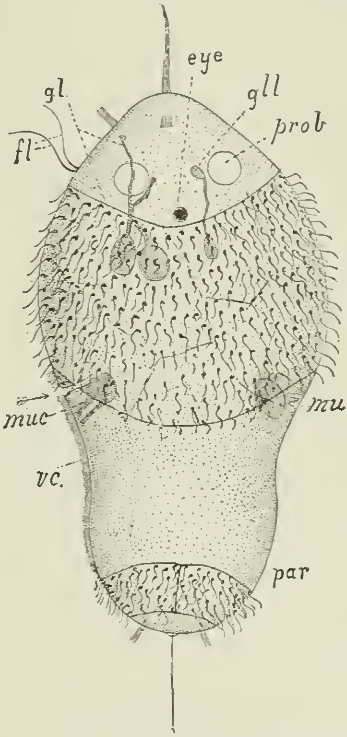

FIG. 15.—*Amphitrite.* Prototroch, paratroch closed ventrally. *muc. gl.*, mucous glands: *fl.*, flagella; *v.c.*, ventral band of cilia: *prob.*, problematic bodies which persist only as long as the prototroch.

Some of the later stages of the trochophore are represented in Figs. 13, 14, 15, and 16. For a considerable time the outlines of the component cells of the prototroch can be distinguished, but in late stages only a few of them can be made out in surface view, though tangential sections prove that they still exist. As the larva elongates, the prototroch extends over more surface, but the cells become thinner. The cilia are fine, not very long, and are thickly and evenly distributed. In the figures they are represented in a purely diagrammatic manner, being much too coarse and not nearly numerous enough to reproduce the actual appearance. When the larva begins to elongate, a second belt of cilia, the paratroch, develops around its posterior end. The paratroch consists of four ciliated cells which are derived from the cell marked d^2 in Fig. 7, p. 117, and, therefore, from that quadrant which did not contribute to the secondary prototroch. At first the four cells lie in a nearly straight row, but the end (lateral) cells gradually approach each other, and finally meet on the ventral side, as may be seen by comparing Figs. 13, 14, 15, and 16. Other cilia and flagella appear in tufts or bands over various parts of the body, while the larva is leading a free-swimming existence; but all these, including prototroch and paratroch, suddenly disappear when the larva, about five or six days old, settles to the bottom.

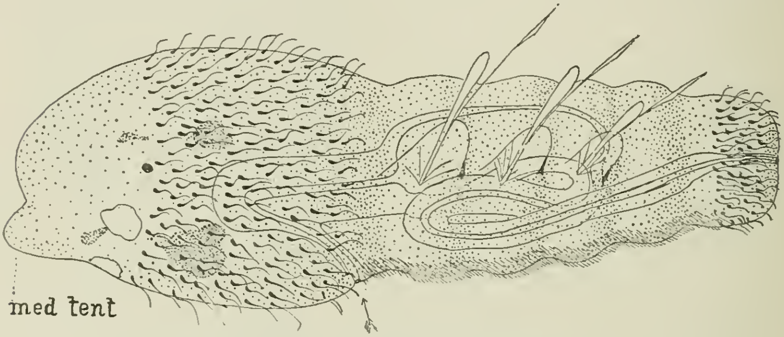

FIG. 16.— Lateral view of *Amphitrite* just before the disintegration of prototroch, paratroch, and mucous glands; *med. tent.*, median tentacle.

Figs. 13–16, when compared with the earlier drawings, illustrate the orientation of the body and the elongation of the trunk. The anterior end is at the left of the picture, the posterior end at the right; the dorsal side at top, and the ventral side at bottom. The anterior end is marked by the polar globules in the earlier drawings, and by the apical tuft of flagella in Figs. 14–16. The median tentacle grows out just ventral to the apical tuft. The posterior end is the middle of the area which becomes enclosed by the paratroch cells, and here the proctodæum is formed (Fig. 16). The "budding zone" lies just in front of the paratroch, and it is by the rapid growth in this region that the trunk elongates. The distance between the prototroch and paratroch, therefore, continually increases.

We stated at the beginning of this paper that, inasmuch as the trochophore is a highly representative larval form, the embryonic origin of one of its essential organs might prove to be of especial value, and the history of the origin of the prototroch in the one species which we have reviewed strengthens this conjecture and brings out some additional points of interest.

The prototroch is differentiated as a definite functional organ at a very early stage in development, when the whole body consists of less than 150 cells. It is composed of comparatively few cells (twenty-five), which are constant in number, in size, in relative position, and in mode of origin, in all individuals of the species. The portion of the larva differentiated as the prototroch is sharply marked off from the surrounding areas by the cell boundaries, and the cells in the immediate vicinity of the prototroch do not especially resemble the latter either in behavior during cleavage or in ultimate function.

Having thus taken our bearings, we find ourselves in this position. The trochophore is a larval form characteristic of a large group of animals, annelids, gasteropods, rotifers, etc., and the prototroch in one species, at least, arises always in the same manner from certain cells through a definite process of cleavage. Although the origin of the prototroch is comparatively simple, yet it is sufficiently complex to offer ample opportunity for variation, and by comparing its cell-origin in other animals we may hope to ascertain whether it always arises from the same cleavage cells. If it does so arise, then we may consider that its component cells are homologous, and, of course, the homology of the prototroch itself will thereby be strengthened. If it arises sometimes from one group of cells and sometimes from another, then its origin may be considered either an accident of the cleavage processes which are without morphological significance, or as indicating that the prototroch is not homologous in the forms examined. To illustrate: let us suppose that we were ignorant of the internal structure of the limb in the vertebrates. This organ, being characteristic of the higher vertebrate body, and having a general external resemblance in different forms, would seem to be homologous throughout the series. Now let us suppose that we have ascertained the origin and arrangement of the component structures of this organ in one species man. If, on comparison with other species, we find that the component structures of the limb have the same arrangement and arise in the same way, we may then consider these parts also to be homologous structures, and the homology of the entire limb is sustained thereby. If, however, we find that the origin of the component structures is essentially different in the various forms, we may then conclude either that the embryonic origin is without morphological significance, or that the limbs themselves are not homologous.

We will begin the comparison of the trochophore of *Amphitrite* with those of other annelids, assuming that the prototroch cells are homologous structures, and, in keeping with the illustration we have just given, we may expect to find:

First, that the particular features of the cell-origin of the prototroch in *Amphitrite* are not the result of the environmental conditions which are peculiar to this egg, but that the same origin obtains in other well-developed trochophores whose environment differs considerably from that of *Amphitrite.*

Second, that in those annelids in which the prototroch is more or less suppressed and develops at a late stage, the cells which we have identified as trochoblasts are small and slow in dividing.

Third, that in distantly related *Trochozoa* which possess a larval structure similar to the annelid prototroch some similarities obtain in the cell-origin of this structure.

Lastly, we might expect that annelid trochophores would be found in which the mode of origin of the prototroch is a modification of that in the assumed type, a modification analogous to that in the skeleton of the vertebrates, due either to the fusion or reduplication of parts.

Fortunately the few annelids in which the cell-origin of the prototroch has been worked out represent different families. *Clymenella*, for example, belongs to the *Maldanidæ*, a family not closely related to the *Terebelidæ* to which *Amphitrite* belongs.

The egg of *Clymenella* is nearly twice the diameter of that of *Amphitrite*, contains more yolk, and develops more slowly. The upper hemisphere is relatively smaller, and there are many minor differences in the rhythm of the cleavage and in the size of the cells. The trochophore is similar in many respects, but is less active. The definitive prototroch, however, consists of twenty-five cells, forming a nearly complete band around the larva. In the 16-cell stage we find the four primary trochoblasts which give rise, by two subsequent cell divisions, to sixteen cells, which constitute the primary prototroch. Each of the three secondary trochoblasts (32-cell stage) divides into a group of four cells, of which three are larger and subequal, while a fourth is small. The three larger cells in each group become ciliated and complete the prototroch, while the small one does not enter into it. *In brief, the origin of the definitive prototroch of Clymenella is identical, cell for cell, with that of Amphitrite.*

In *Arenicola cristata* we have a representative of another family of annelids, the *Arenicolidæ*. The eggs of this worm undergo their early development while encased in a gelatinous capsule, and the cleavage differs somewhat from that of *Amphitrite* and *Clymenella* in rhythm and in the relative size of the blastomeres; but Dr. Child has shown that the primary prototroch and, later, the definitive prototroch originate in precisely the same manner, cell for cell, as in *Amphitrite* and in *Clymenella*.

Though, I think, the cell-origin of the definitive prototroch has not been traced in other annelids, there are records of the mode of origin of the primary prototroch in several.

In *Lepidonotus* it is composed of sixteen cells, which arise exactly as in the annelids just described (see Figs. 6–11, stippled cells). These cells put out cilia very soon after they are formed, as they do in *Amphitrite* (Fig. 10). Later, three of the gaps between the separated portions of the primary prototroch are filled by other ciliated cells, while the mid-dorsal interruption persists just as in Fig. 11 of *Amphitrite*. It is not improbable, therefore, that the *definitive* prototroch of this worm has the same origin as that of other forms. *Lepidonotus* belongs to the *Aphroditidæ;* the eggs are comparatively small, and the cleavage is equal, so that up to the 64-cell stage it is not possible to distinguish one quadrant from another. This fact makes it of especial interest that the gaps in the primary prototroch are filled in only three quadrants instead of in all four, for, if the destiny of the secondary trochoblasts were dependent only upon their *position* in the cell complex, we might expect that the destiny of the corresponding cells would be the same in all four quadrants.

Podarke, which has been described by Treadwell, has a functional primary prototroch of sixteen cells of the same origin as in the other forms just described. (Mr. Treadwell has not yet published the history of the secondary prototrochal cells.) *Podarke* belongs to the family *Nereidæ*. The egg is even smaller than that of *Lepidonotus*, and the cleavage is equal.

Sthenelais, family *Aphroditidæ*, according to Treadwell, also has an equal cleavage, and a functional primary prototroch of sixteen cells is derived exactly as in the five annelids which we have already described.

We may now proceed to those annelids in which the mode of origin of the primary prototroch appears to be a modification of the type. Among these forms *Hydroides* is of special interest.

Wilson and Treadwell have shown that the functional prototroch of *Hydroides* consists of eight cells, two in each quadrant; but the origin of the primary prototroch in *Hydroides* is different from that of *Amphitrite* only in this respect, that the primary trochoblasts divide only once instead of twice. In the seven annelids which we have considered, the primary trochoblasts of the 16-cell stage, stippled in Fig. 8, p. 117, contain material for the prototroch only, and the phenomenon in *Hydroides*, as compared with that of other species, seems to indicate that a cell in which material of a specific structure only is segregated may divide once, twice, or perhaps more times. As long as *all* the descendants of the trochoblasts enter into the formation of the structure in question, it does not matter how many divisions take place. This view is further supported by what has been found in *Capitella*. According to Eisig's recent account, we find in this annelid a modification of the type in the direction of multiplication rather than reduction. Though sixteen cells are produced from the four trochoblasts, and all contribute to the prototroch, they undergo still further division before they become functional.

The first attempt to determine the exact cell-origin of the prototroch was made by E. B. Wilson on the egg of *Nereis*. He described what now seems to be a peculiar variation from the type. The four trochoblasts divide as in *Amphitrite* into sixteen cells, but four of these cells, the upper one in each quadrant, do not enter into the prototroch, but the other twelve cells do so. More cells are subsequently added, but their origin is uncertain. If this account is correct, *Nereis* is the only annelid in which the primary trochoblast has been shown to give rise to other than prototrochal cells.

We may now pass from a comparison of the prototroch and umbrella hemispheres in those annelids which represent the indirect type of development, and examine these features in annelids of more direct development, in which the trochophore is more or less suppressed.

The partially suppressed trochophore of *Scolecolepis* is developed from an egg which contains an abundance of yolk and is protected during its early development within the sand-tube dwelling of the worm. In the 8-cell stage the four anterior cells (upper quartette) are very small in comparison with the four posterior ones. All eight cells divide so nearly at the same time that a 16-cell stage results. Figs. 17 and 18 show that the four stippled cells, which correspond to the primary trochoblasts of other forms, are far smaller than any of the other cells;

not only are they smaller, but they are the most tardy in dividing. After all the other cells have undergone another cleavage, these trochoblasts remain undivided. For this reason the next stage, which is shown in Figs. 19 and 20, consists of but twenty-eight cells instead of thirty-two. Three of these cells correspond exactly, of course, to the secondary trochoblast of *Amphitrite*, *Clymenella*, and *Arenicola*, and are therefore shaded as in Figs. 8 and 9, though they are very small in *Scolecolepis*. Thus in *Scolecolepis* the smallness of the anterior quartette of cells in the 8-cell stage, and the conspicuous minuteness of the trochoblasts, as well as their tardiness in dividing, correspond exactly with the small size of the umbrella of the trochophore and the small size and late development of the prototroch. This annelid, then, in its mode of development stands intermediate between such forms as *Amphitrite* or *Lepidonotus*, which possess a typical trochophore, and *Rhynchelmis* and *Clepsine* (Fig. 22), in which the development is direct and the trochophore undeveloped.

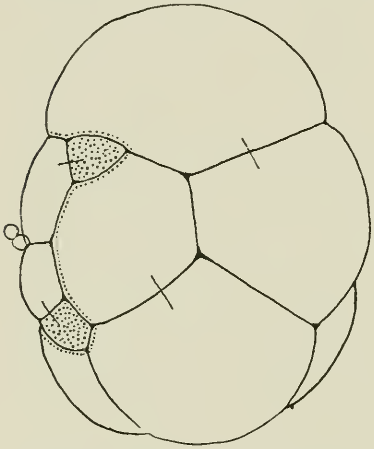

FIG. 17.—*Scolecolepis*, 16-cell stage, left side. Primary trochoblasts stippled; anterior hemisphere (umbrella) bounded by dotted line.

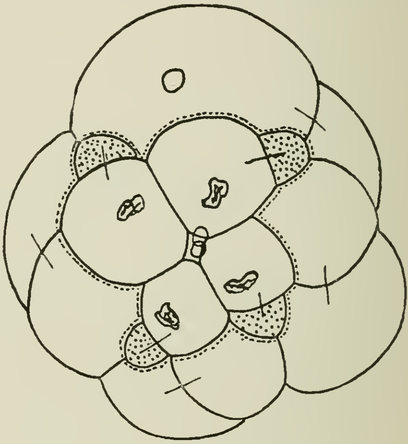

FIG. 18.—*Scolecolepis*, 16-cell stage, seen from anterior end.

Nereis Dummerillii (von Wistinghausen) approaches even nearer than *Scolecolepis* to the direct type. In the former the anterior quartette (umbrella cells) in the 8-cell stage (Fig. 21) are smaller still in proportion to the posterior quartette. With regard to the origin of the prototroch, however, it must be admitted that, according to von Wistinghausen's account, this organ is formed from cells which do not correspond with any of the trochoblasts of other annelids. His account places us in the same predicament with regard to the origin of the prototroch as with regard to the origin of the primary mesoblast cell. In respect to both, if the account is correct, *Nereis Dummerillii* is unique. In order to bring this annelid into line with the others, most writers on cell-lineage have expressed doubt, and rightly I think, as to the accuracy of the account in the case of the mesoblast. The origin of the mesoblast cell, however, is definitely described by von Wistinghausen, while he did not even pretend to work out the prototroch cell by cell. So we may, perhaps, be permitted at least to suspend judgment in regard to the discrepancy in the origin of the prototroch in this species.

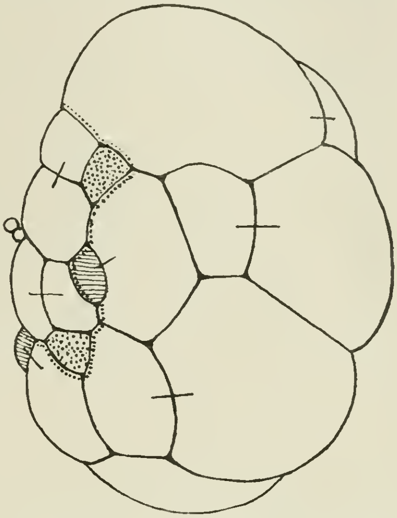
FIG. 19. — *Scolecolepis*, 28-cell stage, from left side. Shaded like figures of *Amphitrite*.

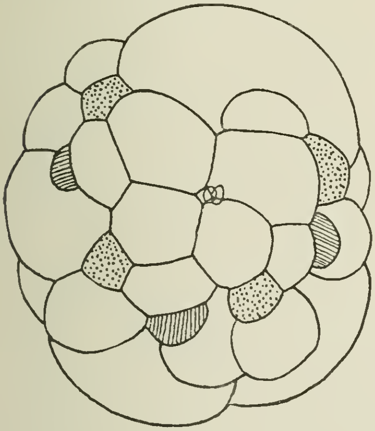
FIG. 20. — *Scolecolepis*, 28-cell stage, from anterior end.

In those annelids in which the trochophore is still farther suppressed, and which undergo a direct development, *e.g.*, in *Rhynchelmis* and *Clepsine*, the anterior quartette in the 8-cell stage is still farther reduced. Fig. 22 is from an unpublished drawing of *Clepsine*, 8-cell stage, given me by Dr. Whitman.

We may say in general of all the forms which we have reviewed, that when the cells of the anterior quartette are comparatively large and divide readily, the umbrella is large and the trochophore active. When, on the other hand, the cells of the anterior quartette are smaller and divide less rapidly, the umbrella is smaller and the trochophore less active. *Lepidonotus*, *Amphitrite*, *Nereis limbata*, *Clymenella*, *Nereis Dummerillii*, *Rhynchelmis*, and *Clepsine* form a series of annelids in which there is a gradual decrease in the relative size and karyokinetic activity of the anterior four cells and a corresponding decrease in the size of the umbrella and the activity of the trochophore.

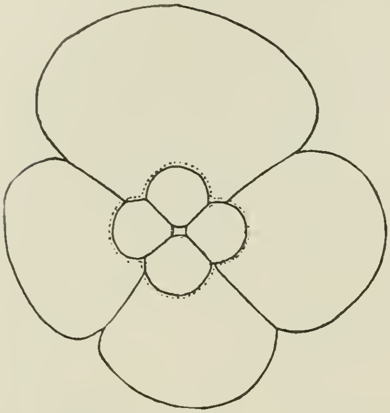

Fig. 21. — *Nereis Dummerillii* (after von Wistinghausen), 8-cell stage, from anterior end ("upper pole").

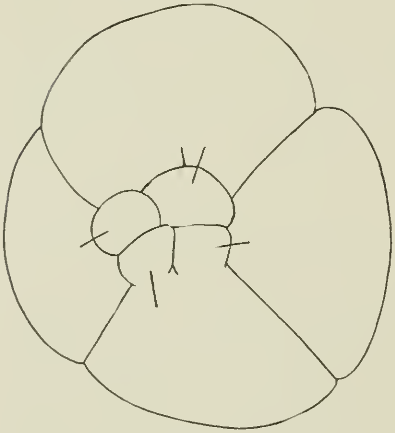

Fig. 22. — Eight-cell stage of *Clepsine* ——. Apical view from drawing furnished by Dr. Whitman.

To sum up: the cell-origin of the prototroch has been completely worked out in three annelids, *viz.*, in *Amphitrite*, *Clymenella*, and *Arenicola*, which represent three distinct families. *In all three the origin of the prototroch is identical, cell for cell. In eight genera of annelids which represent seven families, the whole primary prototroch is formed from identical cleavage cells, the four so-called primary trochoblasts of the 16-cell stage* (Fig. 7), *and all the derivatives of these four cells enter into its formation.* These genera are *Lepidonotus*, *Podarke*, *Sthenelais*, *Hydroides*, *Amphitrite*, *Clymenella*, *Arenicola*, and *Capitella*. In all but two the primary prototroch consists of sixteen cells — in *Hydroides* of eight, and in *Capitella* of more than sixteen. *Nereis limbata* differs from these forms in that four of the sixteen descendants of the trochoblast do not enter the prototroch, and *Nereis Dummerillii* is the only annelid, so far as I am aware, in which the primary prototroch has been thought to arise from other than the primary trochoblasts.

Passing now to other representatives of the branch *Trochozoa,* we have at present among mollusks more or less complete accounts of the cell-origin of the velum, in *Neritina* by Blochmann, in *Crepidula* by Conklin, in *Planorbis* by Holmes (preliminary), and in *Ischnochiton* by Heath (as yet unpublished). The most elaborate published account is given by Conklin in his beautiful work on the gasteropod *Crepidula,* and for this reason we may consider this form first.

Crepidula lays its eggs in capsules, which are protected under the shell of the animal. In two species "it is about four weeks from the time the ova are laid until the fully formed escape from the egg capsules," and probably much longer in other species. Hence it is not surprising that the velum becomes functional at a late period compared with the annelid prototroch, for the annelid begins to swim usually in a few hours after fertilization.

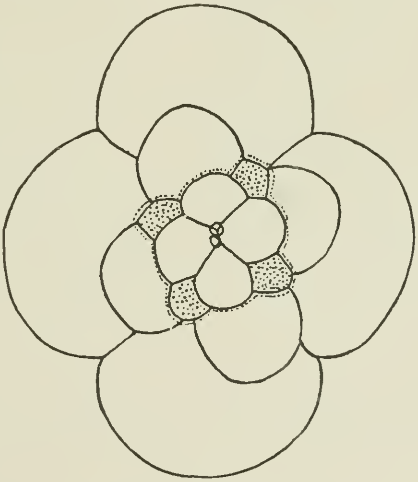

Fig. 23. — *Crepidula*, 16-cell stage, shaded like previous figures, viewed from anterior end.

The general type of cleavage in *Crepidula* is the same as that in the annelids. Fig. 23 of the 16-cell stage of *Crepidula* recalls in particular the same stage in *Scolecolepis,* whose eggs are protected like those of *Crepidula.* In both, the cells of the subumbrella, or posterior hemisphere, are very large and full of yolk, while those of the anterior hemisphere are very small and clear. The cells which correspond to the primary trochoblasts are the smallest of all, and the slowest to divide. In *Crepidula* and in other gasteropods these four cells are known as "turret-cells," but for the sake of uniformity in this paper I will call them primary trochoblasts. They remain undivided, or at most divide only once up to a very late cleavage stage. During these stages, however, they undergo a remarkable growth, so that finally, instead of being the smallest, they are the largest cells in the umbrella. It is the *destiny* of the primary trochoblast, however, which is of special interest to us. On this point Conklin says: "In four species of *Crepidula*, at least the two anterior ones form a portion of the preoral velum (prototroch), and this is probably true of the two posterior ones also." In other words, the primary trochoblasts in *Crepidula* have probably the same destiny as those of the eight genera of annelids mentioned on page 130.

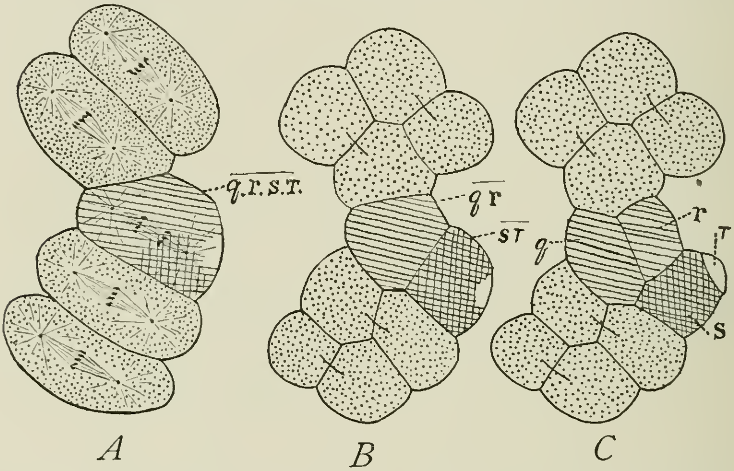

FIG. 24. — Three successive stages, representing the relative position of derivatives of the secondary trochoblast $\overline{q\ r\ s\ t}$ in several forms. Diagram approaches most nearly the condition seen in *Amphitrite*.

We may now consider the behavior of the secondary trochoblasts in *Crepidula* — those three cells of the ideal 32-cell stage, most of whose descendants in *Amphitrite*, *Clymenella*, and *Arenicola* complete the prototroch by filling three of the gaps between its separate parts. *In Crepidula the secondary* *trochoblasts arise in exactly the same manner as in the annelids named, and most, if not all, of their descendants, enter into the prototroch.* This general statement should be qualified by an account of at least some of the details of the later cleavage, in order that it may give a fair idea of the degree of resemblance in question. For this purpose, and to avoid technical expressions, we will make free use of diagrams and arbitrary symbols.

The secondary trochoblast in each of the three quadrants lies between the primary prototroch cells, as in Diagram 24, which is from *Amphitrite* (compare Figs. 8, 10, and 12). It is represented by the compound symbol *qrst.* The phenomena are the same in three quadrants, but the corresponding cells in the fourth quadrant never enter the prototroch. In both *Amphitrite* and *Crepidula* each trochoblast *q*, *r*, *s*, and *t* divides obliquely in the same manner into two cells, *qr* and *st*, the former lying a little anterior to the latter (Fig. 24 *B*). Later, in both animals, each of these two cells divides in the reverse oblique direction, making a group of four cells, *q*, *r*, *s*, *t* (Fig. 24 *C*). In the annelid *q*, *r*, and *s*, soon after their formation, become ciliated and form a part of the prototroch in the manner already described, while *t*, a very minute cell, does not do so. In *Crepidula q* and *r* enter the prototroch ; *s* divides also, its upper product probably entering the prototroch, while the lower product may enter it or may not. The remaining cell, *t*, is very much larger than in *Amphitrite*, and at least part of it probably enters the prototroch, thus giving rise to the only probable discrepancy in the destiny of all the descendants of the primary and secondary trochoblasts in the two forms. What the significance of this discrepancy may be, I will not venture to say, but I wish to call attention again to the fact that the cell *t* in *Amphitrite* is exceedingly small, does not divide for a long time, and has the appearance of a vestigial cell.

It must be said here that Conklin thinks it possible, although by no means certain, that cells other than the trochoblasts enter into the formation of the velum, and in respect to many of the cells which we have already described there is also an element of uncertainty, since the velum of *Crepidula* does not become functional until a very late period of cleavage, so that it is almost impossible to trace its cell-origin accurately.

Blochmann, in his work on *Neritina*, was able to trace the descendants of two cells in the early cleavage into the velum. They could be traced the more readily because of a peculiar texture which distinguished them from the surrounding cells. These two cells in *Neritina* correspond precisely to the two lateral secondary trochoblasts of *Amphitrite* and the other annelids and *Crepidula* (the two lateral cells shaded with lines in Fig. 9). The primary trochoblasts of *Neritina* are also different from the surrounding cells. They are very minute, as in *Scolecolepis*, and were never observed by Blochmann to divide. As far as observations go, therefore, *Neritina* falls in line with the other forms which we have studied.

Conklin has called attention to the altogether characteristic appearance of the primary trochoblast, not only in *Neritina* and in four species of *Crepidula* which he studied, but in *Umbrella* (Heymons), *Urosalpynx*, and *Fulgar*. In all it is conspicuous for its small size, and does not divide for a comparatively long time.

It will appear from Holmes's preliminary paper that the origin of the velum in *Planorbis* bears a remarkable resemblance to that of the annelids. *Planorbis* resembles *Amphitrite* even more than it does *Crepidula* in this respect, *viz.*, the primary trochoblasts are large when formed, and the whole prototroch becomes functional at an early period. With regard to the cell-origin of the prototroch Holmes says: "The prototroch is formed from the [primary] trochoblasts previously mentioned, and the uppermost cells of the second quartette which form the tips of the arms of the cross [secondary trochoblasts, *q*, *r*, *s*, *t*, in the three quadrants]. Possibly other cells of the second quartette may take part in this formation; it is certain that the third quartette has no share in the process."

I am greatly indebted to Mr. Harold Heath for a very complete account of the origin of the prototroch in *Ischnochiton*, and for his courtesy in allowing me to use his discoveries in this paper. The four primary trochoblasts are formed at the 16-cell stage, exactly as in *Amphitrite*, etc., etc. (Fig. 7, stippled cells). These four cells divide into sixteen, all of which enter the prototroch; so far, therefore, the resemblance is complete. The secondary trochoblast also arises in the 32-cell stage, precisely as it does in *Amphitrite*, *Clymenella*, and *Arenicola* (Fig. 8, cell shaded with lines). All of the derivatives of this cell enter the prototroch in *Ischnochiton*, and all but one very minute cell product do so in the annelids named (Figs. 10–12).

The essential features of Heath's account can be most effectively presented by means of diagrams. Fig. 25 represents a lateral view of the prototrochal cells of one side in three stages of development, and the various cells are shaded like those in Fig. 24 (*Amphitrite*). Diagram *A*, Fig. 25, shows the condition of the trochoblasts at about the 32-cell stage. It shows two of the four groups of primary trochoblasts (stippled), each group consisting at this period of two cells, as in *Amphitrite*, etc., Figs. 8 and 24, *A*. Between these cells lies the trochoblast marked *q*, *r*, *s*, *t*. The clear cell marked *x* is a trochoblast, and its two derivatives in each quadrant enter the prototroch,

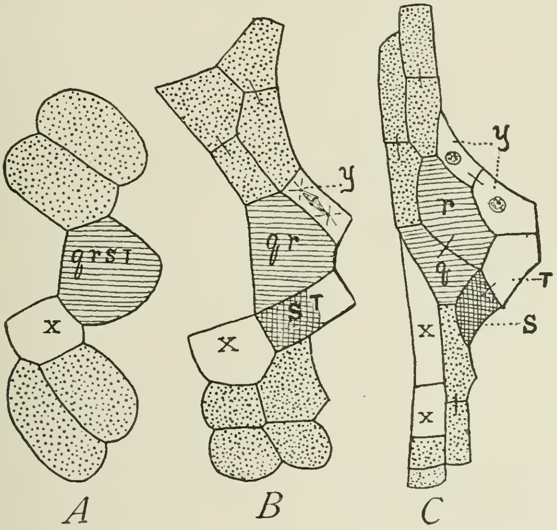

FIG. 25. — Represents trochoblast as seen on left side in *Ischnochiton* (Heath). Three stages shaded like previous drawings. Unshaded cells are not part of the prototroch in the other forms examined. See p. 132.

as may be seen from Diagram *C*. To show the position of this cell in *Amphitrite*, I have marked it *x* in Fig. 10 in one quadrant, and in each of the four quadrants in Fig. 11. If my observations on *Amphitrite* and *Clymenella* and those of Child on *Arenicola* are correct, this cell does not enter the prototroch in these annelids. However, I have never followed its career in either form, except in the posterior quadrant, and here Heath has called my attention to the fact that one of the derivatives of this cell in *Amphitrite* is excessively minute (not as large as a polar globule), and has the appearance, therefore, of a "vestigial cell." As the matter stands at present, this is, I believe, the first important well-sustained discrepancy in the origin of the prototroch, in all the *Trochozoa* which have been studied, and for this reason I would recommend the investigation of the destiny of this cell in the annelids as a fruitful problem in cell-lineage.

Diagrams *B* and *C* in Fig. 25 show that all four derivatives of the secondary trochoblast *q*, *r*, *s*, and *t* enter the prototroch. This is true in three quadrants. It will be recalled that in the three annelids in which these cells are known, *t* is not a prototrochal cell, but is minute and of a vestigial appearance. It is shown in Figs. 11, 12, and 24.

The cell *y* in Fig. 25, Diagram *B*, remains to be discussed. It divides once, and the two daughter-cells take their position in the prototroch, as seen in *C*. This cell *y*, like the cell *x*, does not enter the prototroch in *Amphitrite* (see Fig. 11), *Clymenella*, and *Arenicola*. It is small in *Amphitrite*, but not minute enough to suggest that it is a vestigial cell, though one of its products is distinctly of this appearance. In respect to the cells *y*, *y'*, *t*, and *s*, however, there is an important fact to mention. They are, as far as could be observed, *not ciliated*, and probably serve, Heath suggests, as a sort of supporting layer. For this reason it may, perhaps, be a question whether they should be considered part of the prototroch. If we throw them out, however, there arises another discrepancy between this prototroch and that of the annelid, for in the latter the cell *s* is undoubtedly a part of the prototroch and is ciliated.

For the sake of convenience in comparing the cell-origin of the prototroch in the various annelids and gasteropods in which it has been investigated, we assumed the annelid *Amphitrite* as the type. In this form the prototroch arises from two sources: (*a*) Four cells, primary trochoblasts, one belonging to each quadrant of the umbrella hemisphere, give rise to a functional "primary prototroch," which is for a time the only ciliated portion of the larva. The four cells in question are formed at the 16-cell stage. (*b*) Three cells, secondary trochoblasts, belonging to the right, left, and ventral quadrants of the subumbrella hemisphere, give rise, later, to the rest of the prototroch. These three cells are formed at the 32-cell stage. The whole prototroch is at first interrupted in the mid-dorsal region, but ultimately grows together.

Almost all of the positive evidence furnished by the comparisons which we have drawn points, I believe, to the conclusion, first, that the component cells of the prototroch are homologous in the various types studied, in the same sense as are the component bones in the skeleton of the vertebrate limb. If this conclusion is correct, the homology of the whole prototroch is placed on a firmer basis, and the evidence of the relationship of the two diverse groups of the *Trochozoa* — annelids and mollusks — is likewise strengthened. As a corollary of this conclusion, it would appear that, since certain cells form the same organ under environmental conditions which are unlike, the environmental factors do not have the importance in directly shaping development which is sometimes claimed for them.

Some of the evidence, however, seems to controvert this conclusion. I refer particularly to the discrepancies between Wilson's account of *Nereis limbata* and all other accounts in regard to the destiny of four cells, and to that between Heath's account of *Ischnochiton* and all the other forms in regard to the destiny of four or more cells.

Considering the practical difficulties, we may say with regard to the value of different observations that positive evidence that a certain cell enters the prototroch should have more weight than the negative evidence that it does not, unless a different destiny for the cell is established in the latter instance.

A re-investigation of the prototroch focussed upon these discrepancies would be of great value in determining the trend of the whole mass of evidence, whether it is for or against the doctrines of the homology of cleavage cells, of the significance of cleavage as a factor in differentiation, and of the preorganization of the egg itself.

THE EFFECTS OF CHEMICAL AND PHYSICAL INFLUENCES ON THE DEVELOPMENT OF THE EMBRYO.

By A. D. MEAD.

Transactions of the Rhode Island Medical Society for 1900.

The Effects of Chemical and Physical Influences on the Development of the Embryo.

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THE EFFECTS OF CHEMICAL AND PHYSICAL INFLUENCES ON THE DEVELOPMENT OF THE EMBRYO.*

Forty-two years ago a series of lectures was being delivered before the Pathological Institute of the University of Berlin by Rudolf Virchow, a man pre-eminently distinguished in your fraternity, but one to whom biologists are also greatly indebted. The chief object of the lectures, illustrated as they were by an extensive series of microscopic preparations, was, to use Virchow's words, "to furnish a clear and connected explanation of those facts upon which, according to my ideas the theory of life is now based, and out of which the science of pathology has now to be constructed." "They were more particularly intended to offer in a better arranged form than has hitherto been done a view of the cellular nature of all vital processes, both physiological and pathological, animal and vegetable, so as distinctly to set forth what even the laity have long been dimly conscious of, namely: the unity of life in all organized beings in opposition to the one-sided humoral and neuristical (solidistic) tendencies which have been transmitted from the mythical days of antiquity to our own time: and to contrast with the equally one-sided interpretation of a grossly mechanical and chemical bias the more delicate mechanism and chemistry of the *cell*."

It was in these lectures that Virchow so strongly advocated what he was pleased to call the eternal law of continuous development of all living things whether they be entire organisms or elementary parts. He denied the possibility that cells might arise spontaneously from a ground substance, the *cytoblastema*. "Where a cell arises," he says, "there a cell must have previously existed (*omnis cellulae cellula*), just as an animal can spring only from an animal, a plant from a plant." "Even in pathology we can now go so far as to establish as a general principle that no development of any kind begins *de novo*, and consequently as to reject the theory of equivocal (spontaneous) generation just as much in the history of the development of individual parts as we do in that of entire organisms."

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* Read at the quarterly meeting, March 1, 1900.

Subsequent investigation has substantiated Virchow's thesis, and the study of embryology, as well as that of pathology and of histology, has been pursued from the cell standpoint as revised by Virchow.

Three years later, in 1861, Gegenbaur showed that the ovum even of the hen's egg was a single cell — itself derived on Virchow's formula from a preceding cell in the parent body, and giving rise by successive cell divisions to all the organs and tissues of the offspring. That the successive stages in the development of the embryo simulated the adult form of animals lower in the scale of life had already been formulated as a "law." Also, at this time, Darwin was demonstrating to the world the actual genetic relationship of all animals which have lived and are living. No wonder then that the embryologist now thought that he held the key which would unlock the mysteries of the history of life upon the globe from the earliest times to the present, and that for the next twenty years every effort was bent in this direction! To Haeckel the human unsegmented ovum was the epitome of man's protozoan ancestor, the gastrula represented the jelly fish stage, and the gill clefts of the embryo revealed man's relation to the fishes. In part this may be true; in general it may be said, however, that the aggregate work of the embryologists during those two decades or more resulted to a certain degree in a tragic disenchantment. The embryonic development has been worked out in a great many animals and unquestionably it gives the clue to many relationships, but yet as a precise epitome of the historical record it is veiled by secondary and confusing modifications.

Balked in the attempt to reveal the exact history of life, the ambition of the embryologist has, during the last few years, turned in another direction, namely, toward an explanation of the immediate processes of growth and differentiation, with regard not to the historical significance but to the *modus operandi* of embryonic development.

This new phase of embryology has been termed developmental mechanics. The general problem is this: Are the successive steps in the development of the embryo, up to its specific adult form, pre-determined by an organization in the egg itself; or is the ovum a cell without an organization, an isotropic cell, whose development step by step is controlled by chemical and physical conditions?

Whichever alternative one may be inclined to accept, the cell point of view gives a closer insight into the phenomena of development. The formation of the line of the eye, the formation of the brain, lungs, liver or intestinal canal finds expression in terms of the *uneven* and *peculiar* growth of cells. And so we may ask: Are the form giving peculiarities of the growth and behavior of cells controlled by physical and chemical influences? It is the purpose of this paper to bring together some old and new observations which bear on the affirmative side of this question. A familiar example of the influence of mechanical conditions on cell division is the fact that impact and friction on the palms of the hands induce a rapid proliferation. Again, if the production of chemical substances (internal secretion) is prohibited by the early removal of the sexual organs, the profound modifications which normally occur in the subsequent development of certain structures of the throat and head are prevented. You may, perhaps, question the relevance of these illustrations, but it must be borne in mind that birth or hatching marks no particular stage in embryonic development, for some embryos are hatched or born before the egg is fertilized, or, if you please, are never hatched or born, while others shuffle off the fetal coil at some time from a week to two years after the individual life begins.

The problem of the origin of sex furnishes good material for the study of developmental mechanics. From very early stages the development of the individuals of the two sexes proceeds along diverging courses, so that frequently, as in birds and insects, the adult male and female of the same species resemble each other less than do individuals of different species or even of different genera. Even in man the differences are not inconsiderable. Is the sex of an individual determined by physical or chemical conditions?

Your esteemed colleague, Dr. Schenk of Vienna, has recently aroused in regard to this problem a glow of popular expectation if not of professional interest. It has not been my fortune to have access to Dr. Schenk's book and I am less familiar with the details of his experiment than you are, but I believe that his general conclusion was that the egg will develop into a female when the parent is richly nourished with starch and sugar.

Whether Dr. Schenk be right or wrong the researches of several other investigators leave no reasonable doubt that the sex of many *animals* can be controlled by the early application of physical and chemical agents. The French investigator Maupas has shown that the sex of one of the species of rotifers (Hydatina) can be determined with a great degree of accuracy by subjecting the female parent to different temperatures while the eggs are being formed in the germaria. After this the character of the development cannot be altered by food, light or temperature. In one brood of ten females, five were kept at a temperature of twenty-six to twenty-eight degrees C., and ninety-seven per cent. of the eggs developed into males. The other five were kept at a temperature of fourteen to fifteen degrees C., and only five per cent. developed into males. You will also recollect the classic experiments of Yung on tadpoles. When left to themselves fifty-six per cent. of the tadpoles developed females: when stuffed with highly nutritious food ninety-two per cent. developed into females. In these and other similar experiments it would, therefore, appear that the whole course of development may be directed into this path or that through the influence of external conditions.

Another class of modifications in the embryonic development which requires explanation is the following: Not infrequently there are born among the low animals, as well as in man, individuals of unusual form — abnormalities — freaks of nature — monsters. Are these abnormalities stigmata imposed by the parents upon the offspring and inherent in the very organization of the germinal substance, or are they the results of unusual physical and chemical influences exerted upon the egg or upon the growing embryo? The study of developmental mechanics has thrown at least a beam of light upon this question. The condition of spina bifida for example is occasionally found in the embryos of frogs. Experimenting with these animals Prof. Hertwig of Berlin found that when the eggs were allowed to become over-ripe before they were fertilized (the female frogs being separated from the males for a time) they would frequently develop into embryos with spina bifida. The significance of this observation was enhanced when about two years later Roux observed that the peculiar mutual attraction which he discovered between the living cells of the early embryo was diminished in those embryos developed from over-ripe eggs. Later another observer demonstrated that embryos with spina bifida could readily be obtained from normal eggs and by two different methods, the one chemical, the other physical. If the segmenting eggs be placed in water containing 0.6 per cent. sodium chloride a spina bifida results. In the egg of the frog, as in that of the bird and mammal, the rudiments of the right and left halves of the trunk at first are separate and later meet in the middle line and grow together. This process of concrescence is inhibited in the embryos subjected to the salt solution; each half develops separately, and hence the spina bifida. The other method of producing this condition was that of injuring with a needle that part of the embryo where the rudiments of the trunk first meet.

Another series of most profound modifications of embryonic development has been produced by both chemical and physical influences, namely: the production, from a single normal ovum, of double monsters, twins and even whole litters of embryos. You will recall that among the earliest phases of development is the division of the egg cell (ovum) into two cells: thence it divides into four, eight, and so on with varying degrees of regularity up to many millions. A very neat experiment has been performed upon the frog's egg by Oscar Schulze. In nature this egg is always right side up, being heavily ballasted with yolk. Moreover, of the first two cells, one normally develops into the right half of the tadpole, the other into the left half. Schulze took the egg just as it was going into the two-celled condition, and by an ingenious contrivance inverted it and held it bottom side up. The astonishing result was that each of the two cells, instead of developing into its appropriate half of the embryo, developed into a whole embryo; and from one egg, therefore, two tadpoles arose attached to each other like Siamese twins.

The eggs of some other animals lend themselves to experiment more readily than do those of the frog, from the fact that the cells into which the ovum is at first divided are not so closely pressed together. Such an animal is the primitive fish-like marine vertebrate (Amphioxus). When the egg is in the two-cell stage the cells are easily separated by simply shaking the eggs in a vial of sea water. Each separated cell develops into an embryo of one-half normal size, but apparently normal in every other respect. From one egg, by mechanical interference, separate twins may be derived instead of a single individual. Four embryos, indeed, have been obtained from a single egg by the same method, that is to say, by shaking apart the first four cells.

Another ingenious experiment was contrived by Dr. Loeb of the University of Chicago, whereby he succeeded in producing twins from the unsegmented egg of the sea urchin by the simple expedient of adding a little fresh water to the sea water in which the egg lay. After artificially fertilizing the egg the fresh water was added. The protoplasm absorbed the water to such an extent that it burst the egg membrane and a part flowed out through the rupture. The portion of the protoplasm which was extruded developed into one embryo, and that remaining within the membrane into another. The two remain attached in most cases, sometimes in one way and sometimes in another.

Such experiments as we have briefly sketched indicate clearly that the embryo may be directed into one course or another and profoundly modified through the influence of physical and chemical agents. They furthermore lead naturally to the query: What gives to the ovum in the first place its sudden remarkable energy of growth and development? It seems to be a well-established fact that the human ovum may remain in the ovary for twenty, thirty or even forty years without once dividing, and then when fertilized, it begins a new cycle of divisions which result in the millions of cells in the adult organism. A similar phenomenon occurs in other animals though the latent period may not be so long.

Three years ago I was led to the consideration of this problem while studying the fertilization processes of one of the marine annelids. Here also the eggs remain in the body cavity of the mother for several days at least after they are all ready to develop if fertilized. When at any time some of these eggs are taken out and artificially fertilized, within an hour they begin to segment and in about four or five hours they swim about in the water. Now between the condition of the egg in the body cavity and the first actual segmentation stages there intervenes quite an extensive series of changes, including two cell-divisions (maturation divisions) which are accomplished with the utmost precision by every egg which develops. But these changes will not take place until the spermatozoon enters the egg and the minute it does enter they commence. From certain theoretical considerations I was led to believe that the spermatozoon started up these processes, not by conveying into the egg a new mechanism for division, but by stimulating the mechanism already there. This mechanism, there was reason to believe, was the same in kind as that which is concerned in the protoplasmic contraction of a muscle fibre. At this juncture a friend suggested that I try the effect of a little KCl, $MgCl$ or $CaCl$, as these salts would stimulate the rhythmical contraction of an isolated portion of a turtle's heart that had stopped beating for seventy-two hours. In putting a small amount of KCl into the water the eggs went through these various stages with all the precision and detail of fertilized eggs, so that this chemical stimulus produced exactly the same effect as the spermatozoon through this portion of the development. The eggs, however, did not develop into embryos.

During the past summer Loeb has conducted some similar experiments with much more remarkable results.

According to his account, when unfertilized sea-urchin eggs are brought into a mixture of equal parts sea-water and ten-eighths normal solution of $MgCl$ they not only undergo the preliminary stages but actually develop into embryos with all the characters of those derived from fertilized eggs. During the Christmas Session of the American Society of Naturalists at New Haven, word was received from the Zoological station at Naples that Loeb's experiments had been successfully repeated.

The newspaper accounts of Loeb's experiments has given rise to a popular misconception of their significance, for it was announced in glorious headlines that at last life had been created by chemical means.

The object of this paper is to bring before you some examples of the effect of chemical or physical influences upon the development of the embryo, and in the endeavor to do this I have treated the general problem of development mechanics in a one-sided manner. It is an obvious conclusion that these external influences are potent factors in diverting the development into one course or another and in bringing about other profound modifications. Yet I cannot conclude this paper without the remark that, after all, the most remarkable and impressive feature of embryonic development is the ingenuity and persistency displayed by the organism in striving to reproduce the form and characters of its parent.

THE RAMI OF THE FIFTH NERVE IN AMPHIBIA.

By G. E. COGHILL.

Journal of Comparative Neurology, Vol. XI, No. 1, April, 1901.

THE RAMI OF THE FIFTH NERVE IN AMPHIBIA.

By G. E. COGHILL.

With One Plate.

[Reprinted from the JOURNAL OF COMPARATIVE NEUROLOGY, Vol. XI, No. 1, April, 1900.]

THE RAMI OF THE FIFTH NERVE IN AMPHIBIA.

By G. E. Coghill.

With Plate V

In a study of the components of the cranial nerves of Amblystoma I have found very suggestive relations existing between the ramus ophthalmicus profundus V and the ramus palatinus VII. This observation has led me to review the conditions generally described in Amphibia, and to my own mind the Amblystoma is extremely helpful in interpreting the relations between certain rami of the fifth nerve in Urodela on the one hand and the Anura on the other.

My observations upon Amblystoma tigrinum have been made from serial sections of the heads of larvae of different ages and of the adult head also. The series were cut transversely ten micra thick, and in both planes longitudinally. Those of the larva were hardened in Flemming's stronger solution, diluted in some cases, and stained on the slide after Weigert. The adult head was stained *in toto* according to vom Rath. For comparison I have made also a series, cut transversely, of the head of a larva of Rana at a stage some time previous to the appearance of the hind limbs. This series is absolutely continuous through the region in question and is satisfactorily stained with the Weigert method after fixation of Flemming's stronger solution. It has enabled me to supplement Strong's description of the "accessory rami" of the trigeminus and to show their relation to certain nerves in Amblystoma.

In Amblystoma the lateral line ganglion of the seventh nerve, associated with the Gasserian ganglion, is microscopically distinguishable from the latter. It gives off two rami which arise in close contact with one another from the most dorsal portion of the common ganglionic mass. In the adult these nerves arise wholly separate from any branch of the Gasserian ganglion, and are, therefore, in their proximal portions purely lateral line nerves. In some larval heads I have examined, these nerves are more obscure in their relations than I find them in the adult.

One of these lateral line nerves is the superficial ophthalmic VII (Fig. 4, *os*). It passes laterad out of the cranium in company with other branches from the Gasserian and lateral line ganglion, between the muscles masseter and temporalis, then meso-cephalad subcutaneously mesal of the eye. It innervates the supra-orbital lateral line organs. It is intimately associated with a twig from the opthalmicus profundus V over the nasal septum, but in no case have I found a true anastomosis between these nerves. The ophthalmicus superficialis VII is, therefore, a purely lateral line nerve throughout.

The other nerve issuing from the lateral line ganglion in close relation with the superficial ophthalmic is the ramus buccalis VII. It at first follows a course ventral of the superficial ophthalmic VII, and as it passes out of the cranium fuses with a general cutaneous nerve from the Gasserian ganglion (Fig. 4, *b*). The resulting nerve will be discussed blow.

The dorso-lateral portion of the Gasserian ganglion gives rise to the ramus mandibularis V, which, farther than its origin from the ganglion and its relation to the nerve which joins the buccal VII, has no bearing on the present discussion.

From the ventral portion of the Gasserian ganglion the ophthalmicus profundus V passes directly cephalad, and, after giving off numerous branches of no special significance here, divides in the region of the optic nerve into three terminal branches. These nerves I designate, for purposes of this discussion, as the lateral, mesal and ventral terminal branches of the opthalmicus profundus V (Fig. 1, *ol*, *om*, *ov*).

The mesal terminal branch of the ophthalmicus profundus (Fig. 1, *om*) inclines mesad to a position dorsal of the muscle obliquus superior and mesal of the olfactory epithelium, near the dorsal wall of the olfactory capsule. Within the capsule it gives off several twigs which penetrate the roof of the capsule and are distributed to the skin dorsal of the latter and near the tip of the snout. The terminal twigs of the mesal nerve ultimately reach the skin mesal of the external nares.

The lateral terminal branch (Fig. 1, *ol*) sends a twig to the anterior canthus of the eye, and innervates the skin anterior, not ventral, of this point. In one case I have observed a twig from this nerve anastomosing with a twig from the mesal terminal branch of the ophthalmic, and the resulting nerve going to the skin lateral of the external nares. Terminal twigs of the ophthalmic always innervate the region traversed by the buccalis VII, but they never enter the area innervated by the general cutaneous nerve which accompanies the buccal proximally.

The ventral terminal branch of the ophthalmic (Fig. 1, *ov*) passes ventral of the olfactory epithelium into the region of the palatinus VII which approaches it near the caudal aspect of the internal nares. As the two nerves approach each other both divide (Fig. 1, *p*, *o*). One division of the ventral ophthalmic branch fuses with the lateral division of the palatine (*lp*) and passes laterad immediately caudal of the internal nares (*n*). A part of the resulting nerve inclines caudad, and the remainder turns cephalad along the lateral aspect of the internal nares and innervates the region lateral and anterior of this point. The other division of the ventral ophthalmic branch, in close relation with the mesal division of the palatine, passes cephalad along the mesal aspect of the internal nares (Figs. 1, 4D, *mp*). The two nerves soon fuse and the resulting nerve innervates the region anterior of the vomers.

The remaining nerve (Fig. 4A, *ac*) which concerns this discussion is that branch of the fifth nerve which arises from the dorso-mesal portion of the Gasserian ganglion and mesal of the origin of the mandibularis (*m*). It is a nerve of about the same magnitude as the buccalis VII with which it fuses as it emerges from the cranium. The resulting nerve passes laterad ventral of the ophthalmicus superficialis VII, and turns cephalad around the border of the temporalis muscle to a position ventral of the eye. Near its flexure about the muscle it sends off to the skin of the vicinity a large twig composed of lateral line and general cutaneous fibers. Near this point also the nerve frequently separates into several bundles of fibers which unite again into a common trunk. Other twigs of varied composition are given off in this vicinity, but a general cutaneous twig to the region immediately posterior of the eye and another of the same composition to the under eyelid seem to be constant.

Near the caudal region of the eye this nerve divides into a general cutaneous nerve (Fig. 4C, *ac*) which innervates the lip anterior and ventral of the eye, and a lateral line nerve (*b*) which innervates the line of organs passing ventral of the eye and around the border of the snout. This nerve is the buccalis VII. It seems to me certain that there is at this point of division a complete separation of the general cutaneous from the acustico-lateral component.

In the larva of Rana we find the ophthalmicus superficialis VII holding practically the same relation to the ganglion and to the other nerves proximally as described for Amblystoma, but it passes more directly cephalad in Rana and becomes separated from the other rami much sooner than in Amblystoma (Fig. 3, *os*). The ramus buccalis VII, however, passes around the anterior border of the ear capsule in company with the rami from the Gasserian ganglion in essentially the same relation to them as the buccalis holds to the corresponding nerves in Amblystoma. And, like the buccalis of Amblystoma, the buccalis of Rana soon fuses with a general cutaneous nerve from the Gasserian ganglion (Fig. 3, *b*, *ac*). The further course of the nerve will be considered below.

Arising from the latero-dorsal region of the Gasserian ganglion in Rana we find the maxillo-mandibularis instead of the mandibularis as in Amblystoma, and from this the maxillaris nerve arises at the transverse level of the eye (Figs. 2, 3, *m*, *mx*). The maxillaris gives off a branch ventrally (Fig. 2, *mxc*) which anastomoses with the lateral division of the palatinus VII (Fig. 2, *lp*) in the roof of the mouth near the postero-lateral aspect of the internal nares (*n*). The resulting nerve continues cephalad along the lateral aspect of the internal nares (Fig. 3D, *x*) and is distributed to the antero-lateral areas of the roof of the mouth. The remainder of the maxillaris trunk continues its course cephalad wholly lateral of the olfactory epithelium and is distributed to the skin between the eye and the external nares (Fig. 3D, *mx*). I can find no fibers of the maxillaris going to the eyelids. The region innervated by the nerve corresponds with a part of the region innervated in Amblystoma by the lateral terminal branch of the ophthalmicus profundus (Fig. 4D, *ol*). Moreover, the oral region innervated by the maxillaris through anastomosis with the lateral division of the palatinus VII corresponds with the oral region innervated in Amblystoma by a part of the ventral terminal branch of the ophthalmicus through anastomosis with the lateral division of the palatine.

In perfect accord with the facts just cited we find that in the larva of Rana the ophthalmicus profundus V, in its origin like that of Amblystoma, after giving off several sensory and motor twigs, breaks up into two terminal branches, the lateralis narium to the skin immediately caudal of the external nares, and the medialis narium which passes dorsal of the olfactory epithelium and sends a branch, the ramus communicans cum N. palatino, ventrad to anastomose with the mesal division of the palatinus VII which approaches it from along the mesal aspect of the internal nares (Figs. 2, 3, *mp*). By this anastomosis the oral region is innervated which corresponds to the region innervated in Amblystoma by a part of the ventral terminal branch of the ophthalmicus profundus through anastomosis with the mesal division of the palatinus VII.

Reviewing from another standpoint the conditions just described, we see that the ramus palatinus VII in both Rana and Amblystoma forms into two terminal branches, one of which passes on either side of the internal nares (*mp*, *lp*). In Amblystoma both of these branches anastomose with the ophthalmicus profundus while in Rana the mesal division anastomoses with the ophthalmic and the lateral division with the maxillaris V. Within the oral cavity, therefore, the function of the maxillaris

V of Rana is performed in Amblystoma by the ophthalmicus profundus.

In the light of these facts it becomes impossible to homologize the ventral terminal branch of the ophthalmicus profundus in Amblystoma with the ramus communicans cum N. palatino in Rana. The former nerve is the equivalent of two nerves in Rana, the ramus communicans cum N. palatino of the ophthalmicus and that of the maxillaris.

It is a noteworthy fact, also, that in Rana, according to GAUPP, the maxillaris nerve, in union with fibers from the ophthalmic, innervates the muscle levator bulbi. In Amblystoma this muscle is innervated wholly by the ophthalmic. This is not only another case where the functions of the ophthalmicus profundus in Amblystoma are carried over to the maxillaris in Rana, but it shows that in Rana there is an intimate relation between the maxillaris and ophthalmic nerves, a relation which exists between the general cutaneous as well as between the motor components of the nerves as shown by the anastomoses between the terminal sensory twigs of the two nerves described by GAUPP.

An unqualified homology can not be established between the two species with reference to the other terminal branches of the ophthalmicus profundus. The lateralis narium of Rana is certainly not homologous with the lateral terminal branch of the nerve in Amblystoma, for the latter nerve innervates a region belonging, at least in the greater part, to the maxillaris in Rana. Exact homologies in this region can be established only by far more extensive comparative and perhaps embryological data than have yet been compiled.

The nerve which has usually been called the maxillaris in Urodela is of special interest in this connection. The discovery of a lateral line component in this nerve forced it out of complete homology with the maxillaris of Anura, but some anatomists have called its general cutaneous component the maxillaris. A comparison of this nerve with Strong's lateral "accessory ramus" of the trigeminus as to origin and distribution is quite conclusive.

According to my preparation the lateral and larger "accessory ramus" arises, as Strong describes it, from the dorso-mesal portion of the Gasserian ganglion. It passes across the dorsal surface of the maxillo-mandibularis and passes around the anterior border of the ear capsule ventral of the buccalis VII (Fig. 3, *ac*, *b*, *m*). The buccalis VII and "accessory ramus" pass laterad close together to near the lateral border of the suspensorium. In this position the two nerves are fused for a short distance. Farther cephalad the buccalis holds its usual infra-orbital position. The "accessory ramus" follows close along its lateral aspect to a position ventral of the eye (Fig. 3C, *b*, *ac*).

Soon after separating from the buccalis VII the "accessory ramus" sends off a large branch which passes laterad and cephalad to the skin of the cheek caudal of the eye. Ventral of the eye it sends another branch to the skin of the cheek, and a small twig to the lower eyelid. Ventral of the anterior part of the eye there appears, in close relation with the buccalis VII, a small nerve which arose from the "accessory ramus" a short distance ectal of the Gasserian ganglion and, traversing the surface of the facial muscles, distributes itself to the skin antero-ventral of the eye.

This general cutaneous branch of the trigeminus, therefore, innervates in the larva of Rana the region corresponding to that in Amblystoma innervated by that nerve from the Gasserian ganglion which is fused with the buccal VII. These nerves correspond also in their origin, arising in both cases from the dorso-mesal portion of the Gasserian ganglion and passing across the dorsal surface of the mandibularis in the one case and the maxillo-mandibularis in the other. They correspond also in the relation to the buccal VII, the extent of the fusion being exceedingly reduced in Rana. They correspond also in other details which need not be discussed here. We must conclude, therefore, that the "accessory ramus" of the trigeminus in the tadpole is homologous with the general cutaneous portion of the so-called maxillaris in Amblystoma. This being the case, we have in Amphibia an infra-orbital nerve of acustico-lateral and general cutaneous composition.

The relations of this infra-orbital nerve in the adult Rana seem to be but partially known. The acustico-lateral component degenerates with the disappearance of the lateral line organs. The general cutaneous component probably persists as the rami zygomatico-temporales and palpebrales inferioris as described by Gaupp. The relation which the nerve holds to the maxillo-mandibularis in older tadpoles suggests the possibility of a more extensive fusion of the nerve with that trunk so that the at one time independent twig might later become a ramus of the maxillaris. It is quite certain, at any rate, that the region innervated in the adult by the rami mentioned is not touched by the maxillaris of the larva but is innervated by the "accessory ramus."

Although the relations existing in other Amphibia between the ophthalmicus profundus, the maxillaris, and the palatinus VII have received but incidental notice by anatomists generally, a brief review of the subject may be helpful.

In Siredon pisciformis (larva of Amblystoma) Fischer describes the ventral terminal branch of the ophthalmicus profundus (his nasalis) as issuing from the lateral terminal branch of that nerve. He finds the anastomosis of the ventral branch with the palatinus VII, and describes the nerve resulting from that anastomosis as passing cephalad over the vomer essentially as I find the mesal nerve derived from the double anastomosis. The anastomosing nerves which pass laterad immediately caudad of the internal nares escaped his notice. The infra-orbital nerve, which I have described as composed of acustico-lateral and general cutaneous components, Fischer calls the maxillaris superior of the trigeminus. The peripheral distribution he assigns to this nerve fulfils all the conditions of both components. In Amblystoma punctatum, Herrick describes the ophthalmicus profundus as forming into three terminal branches, and mentions the anastomosis with the palatinus VII as a "broad commissure." His figures suggest that he saw the two nerves, the mesal and lateral, derived from this anastomosis, but he has not shown its real nature. The infra-orbital nerve he calls the maxillaris and assigns it to the trigeminus. He makes this maxillaris homologous with the maxillaris of higher forms.

In Salamandra maculata, according to KINGSLEY's correction of the work of VON PLESSEN and RABINOWICZ, the relations between the nerves in question would seem to be essentially the same as I have described them in Amblystoma tigrinum. However, neither VON PLESSEN and RABINOWICZ nor KINGSLEY describe the compound nature of this anastomosis.

In Cryptobranchus alleghaniensis (Menopoma Harl.) FISCHER describes the first branch (ophthalmicus profundus) of the trigeminus as anastomosing, by a branch given off in the region of the muscle rectus superior, with the second branch (maxillaris) of the trigeminus. WILDER confirms this anastomosis and says that the nerve resulting from it anastomoses through a few fibers with the palatinus VII. McGREGOR, mentioning the anastomosis between the ophthalmic and maxillaris, says nothing of the fibers which enter the palatine. He claims, however, that the presence of lateral line organs ventral of the eye proves the presence of lateral line fibers in the maxillaris (second branch, of FISCHER). If there are such fibers in this nerve it would seem to be homologous with the infra-orbital nerve in Amblystoma, in which case the anatomosis with the ophthalmic would present some difficulty. But McGREGOR does not claim completeness for his work inasmuch as it was mostly done by dissection.

In Amphiuma, according to WILDER, the relation between the ophthalmic and maxillaris are the same as in Cryptobranchus. He describes also a similar anastomosis between the same nerves in Siren lacertina, but none between either the ophthalmic or maxillaris and the palatine.

In Necturus MISS PLATT has observed the ontogenetic development of the nerve which corresponds with the infra-orbital nerve in Amblystoma. She shows that the nerve consists of general cutaneous V and accustico-lateral VII components which are intimately associated in the process of differentiation from the ectoderm. The general cutaneous component of this nerve she makes homologous with STRONG's lateral "accessory ramus" of the trigeminus of the tadpole. If, from her standpoint, MISS PLATT can show that the ontogenetic development of the "accessory ramus" and the buccal VII in the tadpole corresponds with that of the two components of the infra-orbital nerve in Necturus, the evidence will be most conclusive, but she has offered no exact data to sustain the homology. MISS PLATT's suggestion, however, is the only one I have been able to find in the literature as to the representative in Urodela of STRONG's "accessory ramus" in the tadpole.

In Spelerpes bilineatus MISS BOWERS says that the ophthalmicus profundus, near the muscle rectus internus, divides into three branches; but her drawings represent the "middle one of the three branches" as coming off of the mesal or "most dorsal." It is impossible to say which representation is correct. The one in the drawing would sustain her homologies better than the one in the text. But from her descriptions generally I am led to believe that the relations are essentially the same in Spelerpes as I find in Amblystoma. Her diagram of the anastomosis of the ophthalmicus profundus and palatinus indicates that the palatinus divides posterior of the internal nares as it does in Amblystoma, each division receiving fibers from the ophthalmicus profundus. If such is the case, the homologies which she proposes for the terminal rami of the ophthalmicus profundus are extremely doubtful.

In her treatment of the infra-orbital nerve in Spelerpes, MISS BOWERS distinguishes accustico-lateral and general cutaneous components, considering the latter component as representing the maxillaris V. She observes, however, that this nerve does not anastomose with the palatinus VII as the maxillaris does in Rana. In its relation to the buccal VII the general cutaneous portion of this nerve in Spelerpes approaches more nearly the conditions found in Rana than does that of Amblystoma, providing we consider this component as homologous with the "accessory ramus" in the tadpole.

The works reviewed above serve only to show that there are, in the gross structure of different genera of Urodela, variations which, when fully known, may throw light upon the particular points in question. The roots, ganglia and main trunks of the nerves of Amphibia in general have been faithfully dissected, but the finer peripheral relations of these parts demand greater detail in description before any broadly comparative evidence can be deduced upon the questions presented in this paper. The conclusions offered here are, therefore, based wholly upon my own observations and concern only Amblystoma and Rana.

CONCLUSIONS.

1. In both Rana and Amblystoma there are two anastomoses in the roof of the mouth between the general cutaneous component of the trigeminus and the communis component of the facial. These anastomoses take place through the palatinus VII which, in both cases, divides, sending one division lateral and the other mesal of the internal nares.

2. The regions innervated respectively by the mesal and lateral branches of the palatinus VII through anastomosis with the general cutaneous component of the trigeminus correspond in the two genera. The branches of the palatinus VII must, therefore, be homologous each to each.

3. The communicating nerve between the palatinus VII and ophthalmicus profundus V in Rana can not be homologous to the communicating nerve between the nerves of the same name in Amblystoma, since the former anastomoses with but one branch of the palatinus VII while the latter communicates with both branches of that nerve.

4. The anastomosis between the general cutaneous component of V and the lateral division of the palatinus VII takes place through the maxillaris nerve in Rana and through the ophthalmicus profundus in Amblystoma. The function of the maxillaris in Rana is therefore performed in Amblystoma by the ophthalmic so far as the oral cavity is concerned.

5. In cutaneous distribution, also, the function of the maxillaris in Rana is performed by the ophthalmic in Ambly-

stoma. The terminal branches of the ophthalmicus profundus in Rana, therefore, can not be homologized each to each with the terminal branches of that nerve in Amblystoma.

6. As a general conclusion from the above, there is no distinct maxillaris branch of the trigeminus in Amblystoma. The functions of that nerve are performed by the ophthalmicus profundus.

7. The general cutaneous branch of the trigeminus associated with the buccal VII in Amblystoma corresponds to STRONG's lateral "accessory ramus" in the tadpole.

Brown University,
April 3, 1901.

DESCRIPTION OF PLATE V.

Fig. 1. Projection, upon the horizontal plane, of the rami ophthalmicus profundus V and palatinus VII of Amblystoma tigrinum, to show the anastomosis between these nerves.

Fig. 2. Projection of the same nerves of the larva of Rana together with the ramus maxillaris V, on the horizontal plane (after STRONG), to show the character of anastomoses as compared with that in Amblystoma.

Fig. 3. Four transverse sections through the head of a tadpole of Rana, at a stage some time previous to the appearance of the hind legs. Drawn with the camera lucida to show the relations of nerves at various levels.

Fig. 4. Four transverse sections through the head of Amblystoma tigrinum, drawn with the camera lucida, to show the relations of nerves as compared with Fig. 3.

In Figs. 3, 4,

A. Near the anterior end of the Gasserian ganglion, to show especially the relation of *ac* to *m*, *b* and *g*. Fig. 3A is immediately cephalad of the Gasserian ganglion.

B At the level of the passage of *ac*, *b* and *m* around the anterior border of the ear capsule.

C. At the posterior level of the eye.

D. At level of posterior end of internal nares.

REFERENCE LETTERS.

ac.—Ramus of the trigeminus which fuses with buccalis VII.
b.—Ramus buccalis VII.
c.—Brain.
g.—Gassserian ganglion.
l.—Eye.

ln.—Ramus lateralis narium of ophthalmicus profundus.
lp.—Lateral division of the ramus palatinus VII.
m.—Ramus mandibularis V in Amblystoma, maxillo-mandibularis in Rana.
mn.—Ramus medialis narium of ophthalmicus profundus V.
mxc.—Ramus communicans cum N. palatino of maxillaris V.
mp.—Mesal division of ramus palatinus VII
mv.—Mesal division of the ventral terminal branch of the ramus ophthalmicus profundus V.
mx.—Ramus maxillaris V.
n.—Internal nares
o.—Ramus ophthalmicus profundus V.
ol.—Lateral terminal branch of the ophthalmicus profundus V.
om.—Mesal terminal branch of the ophthalmicus profundus V.
os.—Ramus ophthalmicus superficialis VII.
ov.—Ventral terminal branch of the ophthalmicus profundus V.
p.—Ramus palatinus VII.
x.—The nerve formed by anastomosis of *lp* and *ov.*
y.—Nerve formed by anastomosis of *mp* and *ov* in Amblystoma and by *mp* and *mx* in Rana.
z.—Ear capsule.

Fig. 1.

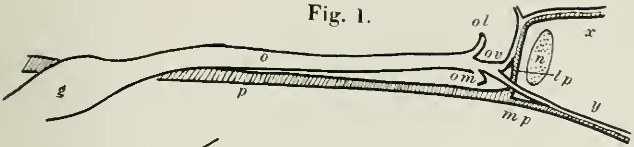


Fig. 2.

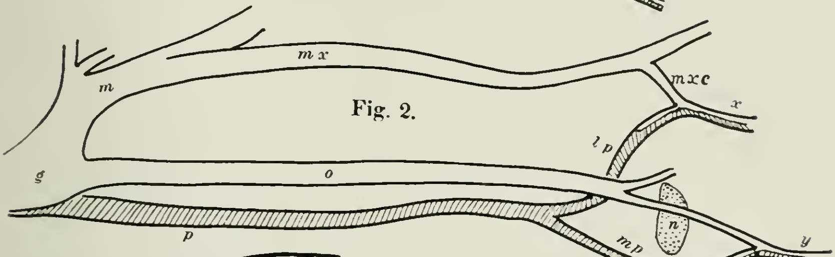


Fig. 4.

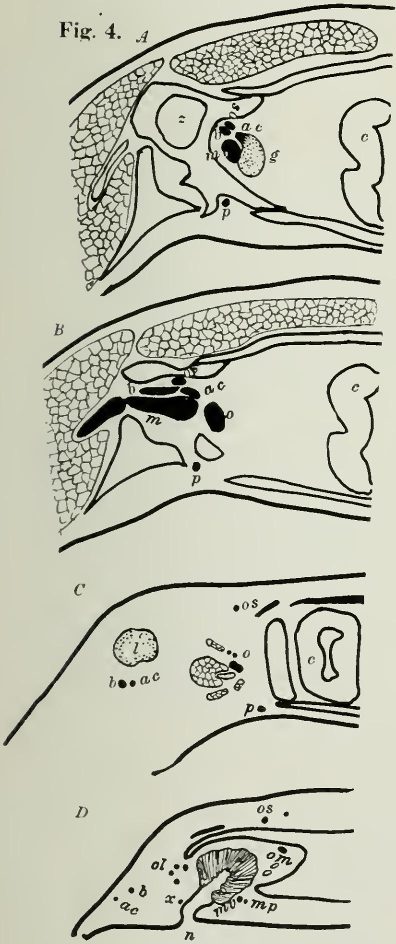
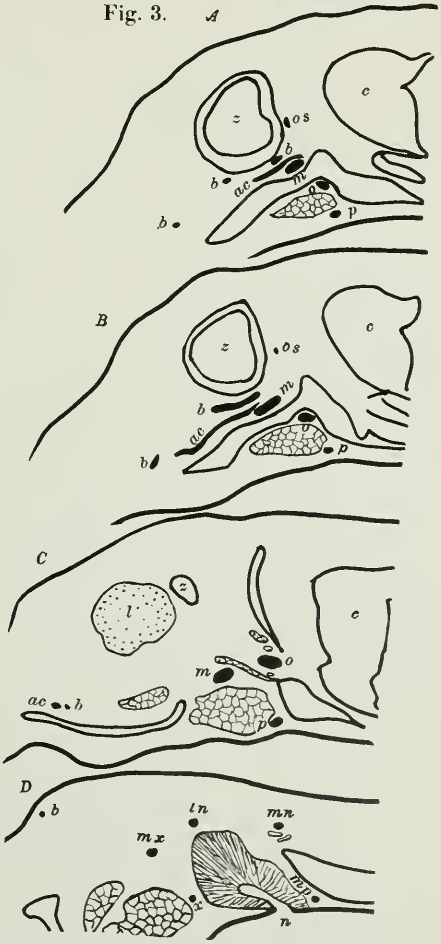


Fig. 3.



THE ELIMINATION OF THE UNFIT AS ILLUSTRATED BY THE INTRODUCED SPARROW, PASSER DOMESTICUS.

By H. C. BUMPUS.

Biological Lectures of the Marine Biological Laboratory for 1898.

ELEVENTH LECTURE.

THE ELIMINATION OF THE UNFIT AS ILLUSTRATED BY THE INTRODUCED SPARROW, *PASSER DOMESTICUS.*

(*A FOURTH CONTRIBUTION TO THE STUDY OF VARIATION.*)

HERMON C. BUMPUS.

We are so in the habit of referring carelessly to the process of natural selection, and of invoking its aid whenever some pet theory seems a little feeble, that we forget we are really using a hypothesis that still remains unproved, and that specific examples of the destruction of animals of known physical disability are very infrequent. Even if the theory of natural selection were as firmly established as Newton's theory of the attraction of gravity, scientific method would still require frequent examination of its claims, and scientific honesty should welcome such examination and insist on its thoroughness.

A possible instance of the operation of natural selection, through the process of the elimination of the unfit, was brought to our notice on February 1 of the present year (1898), when, after an uncommonly severe storm of snow, rain, and sleet, a number of English sparrows were brought to the Anatomical Laboratory of Brown University. Seventy-two of these birds revived; sixty-four perished; and it is the purpose of this lecture to show that the birds which perished, perished not through accident, but because they were physically disqualified, and that the birds which survived, survived because they possessed certain physical characters. These characters enabled them to withstand the intensity of this particular phase of selective elimination, and distinguish them from their more unfortunate companions. It will be convenient for us to arrange our material in the form of tests, as follows.

Test 1: Sex. — It will be noted by reference to the tables that of the *surviving* birds the males are much more numerous than the females. Of the former there are fifty-one (thirty-five adults and sixteen young), while of the latter there are only twenty-one. Among the birds which perished, the females are absolutely and relatively more numerous than they are among the birds which survived, although more than one-half (thirty-six out of sixty-four) of the unfortunate birds are males. Of course it may be that male birds are naturally more abundant than females, but the present question is not one of distribution of sex, but rather of distribution of fitness, and the inference is that the females are less competent to resist severe winter weather than are the males, for, while only 28% of the survivors are females, they constitute 43% of those that perished.

Test 2: Length. — The first column of figures on the several tables gives, in millimeters, the lengths of the birds from the tip of the beak to the tip of the tail. An examination of the averages, printed at the bottom of each column, will prove particularly instructive. It will be noted on Tables I and I^a that the average length of the adult males which survived (159 mm.) is really less than that of the adult males which perished (**162** mm.).[1] Similar figures, 159 mm. and **162** mm. on Tables II and II^a, indicate the same relative lengths of the young males of the two groups. The average lengths of the females of the two groups, 157 mm. and **158** mm., Tables III and III^a, also indicate an excess in the average length of the birds which perished. The birds which perished, then, males or females, adult or young, are longer than those which endured, and we are justified in concluding that when nature selects, through the agency of winter storms of this particular kind of severity, those sparrows which are relatively short stand a better chance of surviving.

Test 3: Alar Extent. — Averages based on measurements from tip to tip of the extended wings fail to bring out any striking difference between the two classes of birds. Both have an indicated average of 2.45 mm., although, to be more exact, the birds which perished averaged 2.449, while those that survived averaged 2.455, a difference too slight to be of material significance. This similarity of the two groups is not to be wondered at, since it is not to be expected that one eliminative agent will express itself in all possible anatomical features. Were the eliminative agent, for example, a severe northerly wind of protracted duration, the alar extent might then enter in as a factor of considerable selective value, and survivors would then have an alar extent materially different from that of the birds eliminated.

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[1] The numbers printed in light type, both in the text and in the tables, refer to birds which survived; those printed in heavy type refer to birds which perished.

The alar extent of the females, corresponding with their smaller size, is less than that of the males.

Test 4: Weight. — Had I been called upon to express an opinion as to whether heavy or light birds would be more successful in resisting the severity of the February storm, I should have declared unhesitatingly in favor of the heavy birds. An examination of the third column of measurements, however, will show that the birds which survived invariably average less in weight than those which perished, and that among the males this difference amounts to more than a gram; that is, to about one twenty-fifth of the weight. The surviving birds of both sexes had an average weight of 25.2 grams, and those which succumbed had an average weight of 25.8 grams.

It may not be out of place to call attention here to certain objections which may be raised to the method which I have adopted, and to the conclusions thus far derived therefrom. One may claim that the greater relative number of females in the group of birds which perished vitiates the numerical result, since the females are of less stature than the males. But it will be noted that this objection answers itself, for the birds which perished are not shorter, but longer, than those which survived; and again, that the birds which perished, though having a disproportionate number of the lighter sex, nevertheless have an average weight considerably greater than that of the birds which survived. Moreover, comparing, in the two groups, adult males with adult males, young males with young males, and females with females, we find that the differences between the two classes of birds are expressed in these three smaller divisions, and I think we are justified in concluding that the differences are really significant.

The explanation that the birds which lived were those which sought, or at least enjoyed, better shelter cannot be entertained, for the storm was of long duration, and the birds were picked up, not in one locality, but in several localities; and, moreover, it is a fact that the survivors are *structurally different* from those which perished. If to these structural characters one desires to add also the intellectual character that the birds knew enough to go in out of the storm, the difference between the two groups becomes so much the greater.

Test 5: Length of Head. — A comparison of the average lengths of head, from the tip of the beak to the occiput, shows only a similarity between the survivors and those which perished, and indicates that under the present environmental conditions this feature is not sufficiently prominent to be expressed by this method of computation.

Test 6: Length of Humerus. — An examination of the fifth column of figures will show that the length of the arm bones of the birds which perished always averages less than that of the survivors. This difference is most conspicuous in the adult males, where the surviving birds have an average length of humerus of .738 of an inch, considerably more than that of their unfortunate companions, .727.

Here again I wish to emphasize the fact that these differences cannot be merely accidental, because they so often tend in the same direction. If among the survivors it is the proper thing for adult males to have a long humerus, then the young males have a long humerus, and the females follow the prevailing fashion with characteristic servitude. If a short humerus is an index of inferiority, all three groups of eliminated birds (adult males, young males, and females) bear this same mark of inferiority. This fact is the more striking since the averages are established on a relatively small number of birds, while usually in the statistical methods of the study of variation an abundance of material is necessary.

Test 7: Length of Femur. — An examination of the general averages on Tables III and III^a shows that the survivors possess longer thigh bones than do the birds which succumbed. The average length of femur in the former is .716 inch; in the latter .709. This difference in the averages cannot be ascribed to the large number of dead females, since the difference prevails also for both the adult and young males.

Test 8: Length of Tibio-Tarsus. — Measurement of the tibiotarsus yields practically the same comparative data as the measurement of the upper bone of the leg, although in both groups of birds this bone in the females is considerably longer than in the adult males, notwithstanding that the females are smaller. This series of measurements agrees with the sixth, in that the young males have longer legs than the adult males.

Test 9. — Measurements across the skull, from the postorbital bone of one side to the postorbital bone of the other, are given in the eighth column, and are less satisfactory, perhaps, than those of other portions of the skeleton. The breadth of the cranium, as thus indicated, is somewhat less in the females than in the males. The averages denote that the birds which survived had wider heads than those which perished, but these averages are considerably influenced by data furnished by the young males. The irregularities in the subordinate groups induce me to place less confidence in these numerical results than in the results from measurements of other structures.

Test 10: Length of Sternum. — This test differs from other tests in that it relates to measurements in the longitudinal axis of the body. In the males the sternum is long, and in the females it is short. In the birds which survived it has a general average length of .845 inch; in those which perished it has a general average length of only .834.

I think these tests prove that there are fundamental differences between the birds which survived and those which perished. While the former are shorter and weigh less (*i.e.*, are of smaller body), they have longer wing bones, longer legs, longer sternums, and greater brain capacity. These characters are in accordance with our ideas of physical fitness; their defective development is evidently a mark of inferiority, and we are justified in concluding that the birds so handicapped failed to pass one of Nature's rigorous tests and perished.

In an earlier lecture, on the "Variations and Mutations of the Introduced Sparrow," facts were adduced which, it was claimed, were sufficient to show that the English sparrow, since its introduction into this country, has found life so easy that the operation of natural selection has been practically suspended, and that the American type consequently has become degenerate. No active agent had eliminated anomalies, and certain "freaks" had increased in number, until they had become over four times as numerous as in England.

When calling attention to the occurrence of these variations, and to the fact that they were an indication of the absence of an active eliminative factor, I little thought that within a few months I might witness the action of an eliminating factor that would test the structural qualifications of *all* the birds: destroy those which had departed unduly from the ideal type, and thus raise the general standard of excellence.

It will be recalled that, after the storm of February 1, one hundred and thirty-six birds were taken, and that, of these, seventy-two revived, while sixty-four failed to recover. But the fact that the birds which perished had in the *average* longer and larger bodies, and shorter head, wing, and leg bones, does not tell all the story of selective elimination.

Reference to the tables will show, not only that the longest bird perished, but also that the shortest bird perished. The longest bird was No. 33, the shortest No. 40. (In these and other cases of extreme departure from the mean, the exponent 1 is placed in the table beside the number of the bird.)

Again, if we examine the columns of figures which indicate the alar extent of the different birds, we find that both the bird with greatest spread of wings, No. 32, and the one with least spread of wings, No. 52, perished.

The heaviest bird, No. 23, weighed 31 grams; it perished. The honors for lightness are evenly divided; No. 53, among the survivors, and No. 60, among the eliminated, have the same weight, *viz.*, 22.6 grams.

The bird (No. 55) whose head was longest (measured from the tip of the beak to the occiput) suffered elimination. The extreme variant in the opposite direction (No. 9) survived.

The honors for the longest humerus, .780 mm., are divided, Nos. 6 and 44. The bird with the shortest humerus, No. 21, perished.

The longest femur was possessed by bird No. 55, the shortest by No. 51.

The surviving birds represent both extremes of variation of the tibio-tarsus (Nos. 18 and 41). In respect to all other columns of measurements the survivors possess exclusively never more than one of the *extreme* forms.

Both extremes of variation in width of cranium (Nos. 55 and 52) are found among the eliminated birds.

The longest sternum is found in one of the surviving birds (No. 15), and it will be remembered that a long sternum was considered a mark of excellence. The shortest sternum (No. 52) is found among the eliminated birds where the standard is low.

These extremes of variation are represented on Table IV, and by counting the dark numbers we find that eleven extreme positions (maximum or minimum) are occupied exclusively by the birds which perished, whereas the light numbers show that only five extreme positions are occupied by those which survived. In two cases (the minimum weight and the maximum length of humerus) the extreme positions are occupied alike by birds of both groups, and consequently I have left the spaces blank. In three cases two birds of the same group occupy the same extreme position, but the table is designed to indicate only the *extreme positions* and not the number of birds occupying them. The *number* of birds occupying these extreme positions is represented on the previous tables by the exponent 1, and if we count up these exponents, we shall find that among the surviving birds there are nine cases of this extreme type, whereas among the birds which perished there are fourteen cases. These numbers are the more impressive when one considers that, inasmuch as there are seventy-two of the former birds and only sixty-four of the latter, the chances for the occurrence of extreme variation are not equal in the two groups.

The birds which perished are at a decided disadvantage because of their smaller representation, yet there are many more "freaks" among them than among the surviving birds.

If it is thought that the association of the larger number of *extreme* variants with the eliminated birds is merely a matter of accident, we will not stop to argue the matter, but will apply the same test to the birds that remain after these extreme examples have been removed. We find even after the removal of these twenty-three examples, that extreme examples of the second order, indicated by the exponent 2, show the same tendency to occur more frequently among the eliminated birds.

The longest birds now are 166 mm.; the shortest, 153 mm. Of the former, Nos. 22, 24, 28, 32, 35, perished, and No. 18 survived; of the latter, Nos. 45 and 62 perished, and Nos. 35, 54, and 55 survived.

If we count the times that the exponent 2 occurs in the tables, we shall find that there are ten birds of extreme abnormality of this second grade which survived, while there are twenty of the same grade which perished.

These figures indicate that the amplitude of variation of the surviving birds is less than that of the birds which perished. Were we to attempt the arrangement of the data into curves of distribution, the curve representing the distribution before the storm would be found to have a broad base, whereas the curve representing the distribution after the storm would be found to have a narrow base, for the eliminative process concentrated its energy on the individuals which occupied extreme positions.

Lest there remain some doubt as to the importance of this eliminative process, and of its efficiency in exterminating extreme variants, let us examine our figures again and see whether the group of birds which has already contributed thirty-four of the extremes of variation has still an excess of variability.

If we count up the exponents (3) of this third order of variable individuals, we find that the birds which survive give eleven examples, whereas those which perished give twenty-one. — It appears unnecessary to carry our investigations further along this line, for our results point always in one direction.

Natural selection is most destructive of those birds which have departed most from the ideal type, and its activity raises the general standard of excellence by favoring those birds which approach the structural ideal.

Inasmuch as the variation in structure in the birds which perished tends to centre about certain individuals, as, for example, Nos. 45, 52, and 55, it might be claimed that the accidental presence of a few of these extremely abnormal individuals in this group is what really makes all the difference. Let us see.

There are twenty-three birds among the seventy-two survivors whose measurements bear exponents of extreme variation, and there are twenty-four birds similarly distinguished among the sixty-four which perished. But none of the birds in the first group has more than three exceptional features, whereas several of the birds which perished have a considerably larger number of exceptional features: four, five, and in one case, No. 52, even six.

Of the twenty-three survivors which bear exponents, nineteen have only one exceptional character, and it is not surprising, considering the high standard of excellence possessed by these birds as a whole, that a single unfavorable feature does not prove fatal. There are but ten of the eliminated birds which have only one exceptional character, and the fact that some are burdened with more than one is apparently the reason for their mortality.

In an earlier contribution to the Study of Variation I called attention to a coincidence which may have considerable significance. When specimens of *Necturus* varied in respect to any one feature, there was a tendency for such specimens to present other and not necessarily correlated variations. Stated in another way, instability in respect to any one feature is an index of general organic instability. A similar coincidence of variations occurs among the sparrows.

Of the one hundred and thirty-six birds, five (Nos. 3, 47, 70, 21, 52) had albino feathers. Like other abnormalities endured by the surviving birds, albinism in two out of the three cases is the only affliction. But among those that were eliminated, where albinism twice occurs, it affects in one case a bird marked by four other abnormalities (No. 21), and in the other a bird (No. 52) already cursed by six abnormalities, the most miserable individual in the entire collection.

While we have shown that the birds which perished have certain average structural peculiarities which distinguish them from the survivors, and that the intensity of selective elimination has been felt most by birds of extreme structure, it remains to be shown that a *general instability* of structure is as characteristic of the birds which perished as a *general stability* of structure is characteristic of those which survived.

If we had sufficient data, this fundamental difference in the two groups of birds might be indicated by curves of distribution, one curve narrow and elevated, showing that its components are closely crowded around an ideal mean, the other broad and low, showing that its components are relatively indifferent to any ideal. But in the absence of sufficient data to illustrate the differences in this manner, we can arrive at a numerical result equally instructive by another method.

Having determined the ideal means for the several characters in each group of birds, we can then find the distance that each individual departs from this ideal. By adding these degrees of departure in respect to the several characters, and dividing by the number of individuals, we shall have numbers which represent the *average* departures from the ideal means. These numbers will be large if the members of a group of birds show a general tendency towards *disregard* of the ideals, and they will be small if the birds tend to crowd around the ideals. If all the birds actually attain the ideals, the number will be zero. — This is simply following out the principle that one man at the end of a ten-foot lever can do as much work as ten men at the end of a one-foot lever. A bird removed ten units from the mean exerts the same divergent influence upon its group that ten birds would exercise if removed one unit.

The results of this test, numerically expressed in Table V, are most instructive. In every case but one the numbers indicating the average departure from the ideal mean are smaller for the birds which survived, and thus indicate a general tendency toward conservatism on the part of the survivors. In the single exceptional case the numbers are not very different, 32 and 31. Granting this exception to the uniformity in the figures, it is exceedingly interesting to examine the series. In respect to length, the birds which perished had an average departure from the ideal mean expressed by the number 3.48, while the average departure of the birds which survived was only 2.51, or, expressed in tabular form:

In respect to length,	3.48	is greater than	2.51.
“ “ “ alar extent,	4.60	“ “ “	4.20.
“ “ “ weight,	12.6	“ “ “	10.9.
“ “ “ length of head,	5.64	“ “ “	5.51.
“ “ “ “ “ humerus,	20.1	“ “ “	16.0.
“ “ “ “ “ femur,	20.0	“ “ “	14.0.
“ “ “ “ “ tibio-tarsus,	33.8	“ “ “	29.4.
“ “ “ width of head,	12.	“ “ “	10., but
“ “ “ length of keel,	31.	“ less “	32.

A series of eight consecutive cases like the above, all pointing in the same direction, can hardly be considered accidental.

To summarize:

(1) We have found that there are fundamental differences between the surviving birds and those eliminated, and we conclude that the birds which survived survived because they possessed certain structural characters, and that the birds which perished perished not through accident, but because they did not possess certain structural characters which would have enabled them to withstand the severity of the test imposed by nature; they were eliminated because they were unfit.

(2) The process of selective elimination is most severe with extremely variable individuals, no matter in what direction the variations may occur. It is quite as dangerous to be conspicuously above a certain standard of organic excellence as it is to be conspicuously below the standard. It is the *type* that nature favors.

(3) Disregard of structural qualifications finally produces a throng of degenerates, whose destruction will follow the arrival of adversity.

TABLE I.

Measurements of Thirty-five Males which Survived.

	Total Length.	Alar Extent.	Weight.	Length of Beak and Head.	Length of Humerus.	Length of Femur.	Length of Tibio-tarsus.	Width of Skull.	Length of Keel of Sternum.
1 ♂	154^{3}	241	24.5	31.2	.687	.668	1.022^{2}	.587	.830
2 ♂	160	252	26.9	30.8	.736	.709	1.180	.602	.841
3 ♂	155	243	26.9	30.6	.733	.704	1.151	.602	.846
4 ♂	154^{3}	245	24.3	31.7	.741	.688	1.146	.584	.839
5 ♂	156	247	24.1	31.5	.715	.706	1.129	.575	.821
6 ♂	161	253	26.5	31.8	.780^{1}	.743	1.144	.607	.893
7 ♂	157	251	24.6	31.1	.741	.736	1.153	.610	.862
8 ♂	159	247	24.2	31.4	.728	.718	1.126	.609	.793
9 ♂	158	247	23.6	29.8^{1}	.703	.673	1.079	.602	.820
10 ♂	158	252	26.2	32.	.749	.739	1.153	.614	.857
11 ♂	160	252	26.2	32.	.741	.723	1.129	.624	.892
12 ♂	162	253	24.8	32.3	.766	.752	1.134	.633	.923^{2}
13 ♂	161	243	25.4	31.8	.721	.722	1.126	.597	.891
14 ♂	160	250	23.7	29.8^{1}	.730	.703	1.103	.590	.820
15 ♂	159	247	25.7	31.4	.729	.717	1.141	.592	.927^{1}
16 ♂	158	253	25.7	31.9	.743	.699	1.150	.600	.860
17 ♂	159	247	26.5	31.6	.733	.714	1.155	.611	.923^{2}
18 ♂	166^{2}	253	26.7	32.5	.767	.765^{2}	1.230^{1}	.600	.878
19 ♂	159	247	23.9	31.4	.752	.723	1.113	.602	.825
20 ♂	160	248	24.7	31.3	.752	.737	1.176	.603	.803
21 ♂	161	252	28.	31.8	.770^{2}	.731	1.190	.590	.885
22 ♂	163	251	27.9	31.9	.769^{3}	.745	1.168	.622	.860
23 ♂	156	242	25.9	32.	.723	.711	1.116	.609	.886
24 ♂	165^{3}	251	25.7	32.2	.751	.742	1.161	.613	.865
25 ♂	160	247	26.6	32.4	.728	.707	1.108	.590	.836
26 ♂	158	244	23.2^{3}	31.6	.730	.713	1.142	.585	.888
27 ♂	160	242	25.7	31.6	.709	.705	1.124	.620	.788
28 ♂	157	245	26.3	32.2	.741	.726	1.143	.595	.850
29 ♂	159	244	24.3	31.5	.723	.698	1.107	.615	.847
30 ♂	160	253	26.7	32.1	.739	.714	1.117	.592	.864
31 ♂	158	245	24.9	31.4	.726	.703	1.119	.580	.854
32 ♂	161	247	23.8	31.4	.735	.694	1.101	.602	.789
33 ♂	160	247	25.6	32.3	.756	.745	1.135	.607	.902
34 ♂	160	247	27.	32.	.755	.736	1.174	.631	.873
35 ♂	153^{2}	241	24.7	32.2	.728	.680	1.092	.592	.884
Average . .	159	247	25.4	31.6	.738	.716	1.135	.602	.857

TABLE I a.

Measurements of Twenty-four Adult Males which Perished.

	TOTAL LENGTH.	ALAR EXTENT.	WEIGHT.	LENGTH OF BEAK AND HEAD.	LENGTH OF HUMERUS.	LENGTH OF FEMUR.	LENGTH OF TIBIO-TARSUS.	WIDTH OF SKULL.	LENGTH OF KEEL OF STERNUM.
1 ♂	165^3	249	26.5	31.	.738	.704	1.095	.606	.847
2 ♂	160	245	26.1	32.	.736	.709	1.109	.611	.842
3 ♂	161	249	25.6	32.3	.743	.718	1.128	.602	.828
4 ♂	162	246	25.9	32.3	.738	.709	1.135	.607	.869
5 ♂	163	250	25.5	32.5	.752	.731	1.197	.623	.888
6 ♂	162	247	27.6	31.8	.731	.719	1.113	.597	.869
7 ♂	163	246	25.8	31.4	.689	.662^3	1.073	.604	.836
8 ♂	161	246	24.9	30.5	.739	.726	1.138	.580	.803
9 ♂	160	242	26.	31.	.745	.713	1.105	.600	.803
10 ♂	162	246	26.5	31.5	.720	.696	1.092	.606	.809
11 ♂	160	249	26.	31.4	.726	.689	1.097	.602	.850
12 ♂	161	250	27.1	31.6	.737	.711	1.120	.631	.852
13 ♂	162	248	25.1	31.9	.744	.722	1.154	.591	.839
14 ♂	165^3	252	26.	32.3	.726	.710	1.145	.609	.887
15 ♂	161	243	25.6	32.5	.709	.707	1.122	.607	.832
16 ♂	161	244	25.	31.3	.702	.685	1.082	.595	.874
17 ♂	162	248	24.6	31.	.713	.700	1.086	.590	.837
18 ♂	164	244	25.	31.2	.703	.690	1.074	.608	.795
19 ♂	158	247	26.	32.	.729	.710	1.145	.607	.803
20 ♂	162	253	28.3	31.8	.752	.718	1.152	.600	.857
21 ♂	156	239	24.6	30.5	.659^1	.658^2	1.042^3	.570^3	.810
22 ♂	166	251	27.5	31.5	.720	.691	1.118	.612	.847
23 ♂	165^3	253	31.^{1}	32.4	.765	.750	1.183	.613	.905
24 ♂	166^2	250	28.3	32.4	.754	.718	1.179	.607	.916^3
Average . .	162	247	26.2	31.6	.727	.706	1.120	.603	.845

TABLE II.

Measurements of Sixteen Young Males which Survived.

	Total Length.	Alar Extent.	Weight.	Length of Beak and Head.	Length of Humerus.	Length of Femur.	Length of Tibio-tarsus.	Width of Skull.	Length of Keel of Sternum.
36 juv. ♂	156	246	24.6	32.	.741	.735	1.167	.592	.849
37 juv. ♂	156	245	25.5	32.1	.761	.717	1.147	.620	.816
38 juv. ♂	163	248	24.8	32.2	.742	.733	1.165	.606	.854
39 juv. ♂	163	248	26.3	33.^{3}	.736	.704	1.148	.609	.839
40 juv. ♂	160	250	24.4	31.5	.746	.715	1.173	.604	.893
41 juv. ♂	156	237	23.3	30.6	.692	.664	1.011^1	.588	.774
42 juv. ♂	162	253	26.7	32.	.759	.734	1.197	.630	.878
43 juv. ♂	163	254^3	26.4	32.	.766	.750	1.165	.605	.886
44 juv. ♂	164	251	26.9	32.	.755	.742	1.171	.620	.886
45 juv. ♂	163	244	24.3	31.3	.718	.680	1.082	.610	.892
46 juv. ♂	160	247	27.	31.5	.764	.732	1.177	.617	.846
47 juv. ♂	160	250	26.8	32.5	.764	.729	1.123	.635^3	.842
48 juv. ♂	158	247	24.9	32.4	.745	.724	1.139	.588	.865
49 juv. ♂	158	249	26.1	32.2	.742	.736	1.148	.602	.817
50 juv. ♂	158	243	26.6	32.4	.747	.711	1.163	.612	.891
51 juv. ♂	155	237	23.3	30.2^3	.685	.653^1	1.011^1	.587	.794
Average . .	159	246	25.4	31.8	.741	.716	1.136	.607	.851

Table II^{a}.

Measurements of Twelve Young Males which Perished.

	Total Length.	Alar Extent.	Weight.	Length of Beak and Head.	Length of Humerus.	Length of Femur.	Length of Tibio-tarsus.	Width of Skull.	Length of Keel of Sternum.
25 juv. ♂	160	249	24.2	30.4	.740	.717	1.130	.620	.840
26 juv. ♂	156	236	26.8	$30.^{2}$	.690	.671	1.067	$.563^{2}$	.832
27 juv. ♂	158	240	23.5	31.	.715	.702	1.113	.595	.805
28 juv. ♂	166^{2}	245	26.9	31.7	.715	.695	1.107	.601	.847
29 juv. ♂	165^{3}	255^{2}	28.6	31.5	.766	.744	1.175	.613	.854
30 juv. ♂	157	238	24.7	31.2	$.680^{3}$	.677	1.156	.599	.769
31 juv. ♂	164	250	27.3	31.8	.764	.726	1.171	.588	.860
32 juv. ♂	166^{2}	256^{1}	25.7	31.7	.752	.751	1.187	.595	.858
33 juv. ♂	167^{1}	255^{2}	$29.^{3}$	32.2	.765	.745	1.197	$.638^{2}$	.855
34 juv. ♂	161	246	25.	31.5	.739	.707	1.123	.587	.850
35 juv. ♂	166^{2}	254^{3}	27.5	31.4	.760	.742	1.124	.604	.914
36 juv. ♂	161	251	26.	31.5	.731	.707	1.122	.589	.828
Average . .	162	248	26.2	31.5	.734	.715	1.141	.599	.842

Table III.

Measurements of Twenty-one Adult and Young Females which Survived.

	Total Length.	Alar Extent.	Weight.	Length of Beak and Head.	Length of Humerus.	Length of Femur.	Length of Tibio-tarsus.	Width of Skull.	Length of Keel of Sternum.
52 ♀	156	245	25.3	31.6	.729	.710	1.152	.620	.809
53 ♀	154^3	240	22.6^1	30.4	.705	.686	1.103	.584	.770
54 ♀	153^2	240	25.1	31.	.724	.713	1.123	.585	.812
55 ♀	153^2	236	23.2^3	30.9	.698	.678	1.132	.596	.795
56 ♀	155	243	24.4	31.5	.734	.736	1.170	.596	.801
57 ♀	163	247	25.1	32.	.748	.734	1.166	.602	.821
58 ♀	157	238	24.6	30.9	.726	.727	1.175	.588	.797
59 ♀	155	239	24.	32.8	.732	.742	1.175	.601	.835
60 ♀	164	248	24.2	32.7	.752	.752	1.201	.604	.830
61 ♀	158	238	24.9	31.	.741	.689	1.091	.592	.866
62 ♀	158	240	24.1	31.3	.733	.706	1.107	.591	.867
63 ♀	160	244	24.	31.1	.731	.730	1.152	.589	.808
64 ♀	161	246	26.	32.3	.758	.732	1.154	.623	.859
65 ♀	157	245	24.9	32.	.752	.740	1.186	.593	.787
66 ♀	157	235	25.5	31.5	.712	.704	1.132	.611	.781
67 ♀	156	237	23.4	30.9	.708	.691	1.123	.613	.798
68 ♀	158	244	25.9	31.4	.729	.705	1.146	.597	.851
69 ♀	153^2	238	24.2	30.5	.715	.707	1.116	.595	.821
70 ♀	155	236	24.2	30.3	.727	.705	1.120	.585	.790
71 ♀	163	246	27.4	32.5	.732	.711	1.163	.630	.862
72 ♀	159	236	24.	31.5	.709	.713	1.129	.607	.845
Average . .	157	241	24.6	31.4	.728	.714	1.143	.600	.819
General average for 72 birds . . .	158	245	25.2	31.6	.736	.716	1.138	.603	.845

TABLE III^{a}.

Measurements of Twenty-eight Adult and Young Females which Perished.

	TOTAL LENGTH.	ALAR EXTENT	WEIGHT.	LENGTH OF BEAK AND HEAD.	LENGTH OF HUMERUS.	LENGTH OF FEMUR.	LENGTH OF TIBIO-TARSUS.	WIDTH OF SKULL.	LENGTH OF KEEL OF STERNUM.
37 ♀	155	240	26.3	31.4	.709	.710	1.125	.614	.815
38 ♀	156	240	25.8	31.5	.715	.678	1.127	.597	.812
39 ♀	160	242	26.	32.6	.740	.732	1.157	.597	.854
40 ♀	152^{1}	232^{3}	23.2^{3}	30.3	.676^{2}	.683	1.048	.590	.780
41 ♀	160	250	26.5	31.7	.741	.731	1.187	.615	.886
42 ♀	155	237	24.2	31.	.727	.723	1.118	.610	.787
43 ♀	157	245	26.9	32.2	.766	.751	1.227^{2}	.620	.841
44 ♀	165^{3}	245	27.7	33.1^{2}	.780^{1}	.757^{3}	1.195	.633	.895
45 ♀	153^{2}	231^{2}	23.9	30.1	.680^{3}	.662^{3}	1.042^{3}	.592	.781
46 ♀	162	239	26.1	30.3	.709	.685	1.092	.587	.911
47 ♀	162	243	24.6	31.6	.741	.729	1.162	.605	.840
48 ♀	159	245	23.6	31.8	.727	.700	1.129	.610	.855
49 ♀	159	247	26.	30.9	.711	.666	1.098	.580	.749^{2}
50 ♀	155	243	25.	30.9	.730	.711	1.127	.598	.839
51 ♀	162	252	24.8	31.9	.752	.738	1.180	.615	.875
52 ♀	152^{1}	230^{1}	22.8^{2}	30.4	.682	.664	1.042^{3}	.551^{1}	.734^{1}
53 ♀	159	242	24.8	30.8	.717	.667	1.090	.575	.809
54 ♀	155	238	24.6	31.2	.706	.702	1.102	.588	.758^{3}
55 ♀	163	249	30.5^{2}	33.4^{1}	.767	.767^{1}	1.207^{3}	.640^{1}	.896
56 ♀	163	242	24.8	31.	.713	.713	1.128	.607	.813
57 ♀	156	237	23.9	31.7	.718	.716	1.090	.611	.800
58 ♀	159	238	24.7	31.5	.726	.701	1.145	.600	.800
59 ♀	161	245	26.9	32.1	.751	.704	1.142	.607	.819
60 ♀	155	235	22.6^{1}	30.7	.695	.692	1.119	.584	.771
61 ♀	162	247	26.1	31.9	.751	.735	1.157	.618	.802
62 ♀	153^{2}	237	24.8	30.6	.732	.718	1.172	.594	.802
63 ♀	162	245	26.2	32.5	.728	.731	1.102	.614	.832
64 ♀	164	248	26.1	32.3	.739	.707	1.159	.592	.823
Average . .	158	241	25.3	31.4	.726	.709	1.131	.601	.820
General average for 64 birds . . .	160	245	25.8	31.5	.728	.709	1.128	.601	.834

TABLE IV.

The Maximum and Minimum Measurements.

	Total Length.	Alar Extent.	Weight.	Length of Beak and Head.	Length of Humerus.	Length of Femur.	Length of Tibio-tarsus.	Width of Skull.	Length of Keel of Sternum.
Maximum . .	167	256	31	33.4	(*d*)	.767	1.230	.640	.927
Minimum . .	(*a*) 152	230	(*b*)	(*c*) 29.8	.659	.653	(*c*) 1.011	.551	.734

(*a*) The minimum length (152 mm.) occurs twice among the birds which perished : Nos. 40 and 52.

(*b*) The minimum weight (22.6 grams) occurs in each group : Nos. 53 and 60, and therefore is not entered.

(*c*) The minimum length of head (29.8 mm.) and of tibio-tarsus (1.011 inch) occurs twice among the surviving birds : Nos. 9 and 14, 41 and 51.

(*d*) The maximum length of humerus (.780 inch) occurs in each group : Nos. 6 and 44, and therefore is not entered.

TABLE V.

Average Departures from Ideal Mean.

	Total Length.	Alar Extent.	Weight.	Length of Beak and Head.	Length of Humerus.	Length of Femur.	Length of Tibio-tarsus.	Width of Skull.	Length of Keel of Sternum.
Seventy-two which survived	2.51	4.20	10.9	5.51	16.	14.	29.4	10.	32.
Sixty four which perished	3.48	4.60	12.6	5.64	20.1	20.	33.8	12.	31.

FACTS AND THEORIES OF TELEGONY.

By H. C. BUMPUS.

American Naturalist, Vol. XXXIII, No. 396, December, 1899.

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FACTS AND THEORIES OF TELEGONY.

HERMON C. BUMPUS.

It will be remembered that Professor Weismann, in a chapter of *The Germ-Plasm*, entitled "Doubtful Phenomena of Heredity," referred to what is generally known as *infection of the germ*, and gave to it the term "Telegony." Although he expressed some doubts as to the existence of the phenomenon, believing that the recorded instances of "infection" were based upon an insufficiency of data or misinterpretation of facts, he felt justified in considering its occurrence *possible*, since supposed cases of infection had been often discussed, and even Darwin had considered the subject worthy of special mention.

The belief that the male of the first coitus may influence the color, structure, and disposition of the young born to a female, of another sire, is almost universally held by stock-breeders, and so tenaciously that even the accidental contamination of a pure-bred female by a male of inferior blood renders her permanently undesirable for breeding purposes.

The question, however, had received no special attention from biologists previous to the Spencer-Weismann controversy of 1893. At that time Spencer accepted telegony as an incontestable fact, called attention to experiments made by Mr. Nouel upon sheep, and described in the *Journal of the Royal Agricultural Society* for 1853; to others made upon pigs by Daniel Giles, Esq., and reported in the *Philosophical Transactions* for 1821; and to the famous experiment of Lord Morton, in which a nearly full-blooded Arabian mare, having been mated to a quagga, by which she had a hybrid foal, subsequently bore to a full-blooded Arabian stallion two foals, which were said to simulate the markings of the quagga. He concluded: "And now, in presence of these facts, what are we to say? Simply that they are fatal to Weismann's hypothesis. They show that there is none of the alleged independence of the reproductive cells; but that the two sets of cells are in close communion. They prove that while the reproductive cells multiply and arrange themselves during the evolution of the embryo, some of their germ-plasm passes into the mass of somatic cells constituting the parental body, and becomes a permanent component of it. Further, they necessitate the inference that this introduced germ-plasm, everywhere diffused, is some of it included in the reproductive cells subsequently formed. And if we thus get a demonstration that the somewhat different units of a foreign germ-plasm permeating the organism, permeate also the subsequently formed reproductive cells, and affect the structures of the individuals arising from them, the implication is that the like happens with those native units which have been made somewhat different by modified functions: there must be a tendency to inheritance of acquired characters."

Romanes expressed himself more cautiously. While admitting that telegony occurred, he questioned its frequent occurrence, and could not accept Spencer's explanation, nor agree with him that the phenomenon disproved Weismann's doctrine of the isolation of the germ-plasm.

In 1896 Dr. A. L. Bell published an article in the *Journal of Anatomy and Physiology*, in which he described several cases that purported to illustrate the influence of a previous sire, and described several experiments that he had made upon horses and dogs for the express purpose of producing results which might be attributed to the influence of telegony. In the same year Karl Pearson examined the matter statistically, and showed that in man there was no evidence that the younger children of a family have characters more nearly resembling those of the father than do the eldest, for it is evident that if telegony really occurs the later offspring of the "infected" mother would resemble the father more than would the first-born.

Mr. Bulman has more recently called attention to the bearing that "hybrid-oölogy" has upon the question of telegony. The eggs deposited by a female bird of a certain species, after she has been mated to a male of another species, will often resemble, in their coloration, the eggs of the latter species. This fact, which appears to be well established, has been thought to prove that the sperm influences not the ovum alone, but the walls of the oviduct, which in turn imprint their acquired character upon the eggshell. It seems to the writer, however, that one is not driven to accept such a phenomenon as an instance of "maternal infection." The hen's egg is not the product of the undirected metabolic activity of the hen alone, but is the result of the joint activity of the combined oöcyte and sperm, — the oösperm, — and the coverings of the egg, the membranes and shell, in their elaboration, must be affected as well by the centrifugal influence of the oösperm as by the centripetal influence of the oviducal walls. The egg takes unto itself what it selects, not merely what is thrust upon it.

A paper strongly in favor of telegony, and partially based upon experiments, was written by Mr. Frank Finn, at the time of the Spencer-Weismann controversy, and published in *Natural Science.* The observations therein recorded, especially those upon varieties of the domestic fowl, are exceedingly interesting, and one would almost become convinced, had the experiments been made for the express purpose of securing definite data bearing upon the disputed question, and had adequate precautions been taken for the exclusion of errors. But it is this very lack of definite data, and the frequent admission of evidence based upon anecdotes and traditions of obscure origin, that have made so many of the communications inconclusive and unsatisfactory. Of an entirely different nature are the efforts of Professor J. C. Ewart of the University of Edinburgh, who has lately published some of the results of his "Penycuik Experiments"; but although his work has received the well-merited attention of the British journals, American publications have been almost shamefully indifferent to its importance.

Professor Ewart began his experiments in 1895, when he secured three male Burchell's zebras. Two of these died, but the third became thoroughly acclimated. This zebra was mated to Mulatto, a black West Highland pony, and the hybrid colt Romulus, born in August, 1896, was even *more profusely striped* than the sire, which in its figure and general behavior it strongly favored. Now, following Lord Morton's experiment, Mulatto was sired by an Arabian horse, and, lo! and behold! like Lord Morton's colt, Mulatto's foal presented a number of stripes, although these were indistinct and visible only in certain lights. A third foal, born to Mulatto in May of the present year by a West Highland pony, Loch Corie, also showed indistinct markings.

It would thus appear at first sight that Mulatto's second and third foals lend support to the belief in telegony, but the Scotch professor did not stop here. Soon after the birth of Mulatto's third foal, two West Highland mares, similar to her, but neither of which had ever seen a zebra, had colts by Loch Corie, both of which were striped. It is thus seen that striped colts may be born to full-blooded parents without the "infection" of a zebra sire, and we are practically forced to give up our interest in the offspring of Lord Morton's mare.

Further experiments of Professor Ewart are as follows: A Shetland mare, mated to a black Shetland pony, had as her first foal a colt distinctly striped. Mated to the zebra, her second foal was the most zebra-like of all of Professor Ewart's hybrids; but when again mated, to a Welsh pony, her third foal, born after she had had an opportunity to become infected by the zebra or its hybrid foal, did not begin to have the conspicuous zebra-like markings of the first foal.

The crossing of Iceland, Irish, English thoroughbred and Arabian mares with the zebra, and the breeding of them subsequently to their own or closely related varieties, failed to afford the slightest evidence in support of the theory of the infection of the germ.

Although the "Penycuik Experiments" were evidently undertaken for the express purpose of proving the truth or falsity of the supposed phenomena of telegony, Professor Ewart struck upon certain by-products of no inconsiderable scientific value. It will be recalled that the existing striped horses are grouped under four species: the quagga (*E. quagga*) of South Africa, the most ass-like, and the one of Lord Morton fame; Burchell's zebra (*E. burchellii*), the species used by Professor Ewart, and occurring on the plains north of the Orange River; the true zebra, or mountain zebra (*E. zebra*), and the Somali zebra (*E. grevyi*) of Northeastern Africa. Professor Ewart is of the opinion that, as far as the coloration is concerned, the last is the most primitive of living zebras, and the colors and markings of the hybrid foals resemble those of this species rather than the color-pattern of their sire. In other words, the process of hybridization results in the resurrection of ancestral characters which have long remained latent, and his experiments show also that even the mere crossing of varieties, or the in-breeding of domestic animals may lead to the production of offspring possessing characters which are to be explained only on the principle of reversion.

Turning to Darwin's *The Variation of Animals and Plants under Domestication*, we read under the caption "Crossing as a Direct Cause of Reversion":

"It has long been notorious that hybrids and mongrels often revert to both or to one of their parent forms, after an interval of from two to seven or eight, or, according to some authorities, even a greater number of generations. But that the act of crossing in itself gives an impulse toward reversion, as shown by the reappearance of long-lost characters, has never, I believe, been hitherto proved. The proof lies in certain peculiarities which do not characterize the immediate parents, and therefore cannot have been derived from them, frequently appearing in the offspring of two breeds when crossed, which peculiarities never appear, or appear with extreme rarity, in these same breeds, as long as they are precluded from crossing."

Lord Morton's mare was used by Darwin in this chapter, not because of its telegonous young, but because its first foal, the hybrid, had stripes "*more strongly defined and darker than those on the legs of the quagga.*" Professor Ewart, not alone by his experiments upon horses and zebras, but by experiments upon pigeons, fowl, and rabbits, has provided an abundance of evidence to prove the correctness of Darwin's views as set forth in this chapter, but he certainly shows that Darwin spoke with insufficient evidence when he said: "There can be no doubt that the quagga affected the character of the offspring subsequently begot by the black Arabian horse." His experiments, moreover, have yielded most welcome information of a definite nature respecting the benign and baneful effects of inbreeding, the unsettled questions bearing upon sterility and the strange phenomena which are associated with the word "prepotency." Both men of science and those interested in the practical occupation of breeding owe a debt of gratitude to Professor Ewart, an obligation that J. Arthur Thomson has acknowledged in a recent article in *Natural Science*, but a testimonial even more fitting would be the adoption of similar lines of research by our numerous and amply equipped agricultural schools and experiment stations. The vexed problems of heredity never will be solved until a great many individuals or institutions seriously undertake experimental breeding.

BROWN UNIVERSITY, Nov. 1, 1899.

ON THE IDENTIFICATION OF FISH ARTIFICIALLY HATCHED.

By H. C. BUMPUS.

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ON THE IDENTIFICATION OF FISH ARTIFICIALLY HATCHED.

HERMON C. BUMPUS.

ALTHOUGH the United States Fish Commission has annually hatched and planted many millions of young fish, and although the planting has often resulted in the apparent increase in the number of adults where the plantings have been made, there is nothing but circumstantial evidence to show that the fish appearing in increased numbers are really the adults of the young artificially produced. The recent excessive abundance of cod along the shores of New England is probably the result of extensive operations at the Woods Holl hatchery. The facts that these fish were small when they first appeared, that they have since increased in size, that they have occurred in localities where cod had never before been caught, and that they are reported to be of a different color from the native variety are interesting, although to the sceptical they are not absolutely convincing. There is need of some scheme whereby the adults of fish hatched artificially may be distinguished from those native to the locality.

To mark the fry is, of course, out of the question, but is it not possible that the fry mark themselves, *i.e.*, is there not a slight difference between the fish of the same species but of different localities, and if there is this slight difference, does it not present itself in a measurable manner?

The careful examination of a large number of periwinkle shells[1] (*Littorina littorea*) has shown that localities even near together are characterized by shells of different proportions. This fact has warranted the examination of a number of fish for the purpose of seeing if they too are not subject to similar varietal changes.

During the latter part of March of the present year, while at the Laboratory of the United States Fish Commission, I examined several hundred winter flatfish (*Pleuronectes americanus*) with the following results :

---

[1] *Zoölogical Bulletin*, vol. i, No. 5, February, 1898, p. 247.

Of 100 flatfish collected at Woods Holl, only one had 62 dorsal fin-rays, seven had 63, twelve had 64, twenty-two had 65, etc., as represented by the ordinates of curve *A* in Fig. 1. The amplitude of variation is between 62 and 72, the arithmetical mean being 66, represented by the vertical line at the right of 66.1, curve *A*. The curve drawn through the upper ends of the ordinates represents graphically the distribution of the 100 variants around this mean.

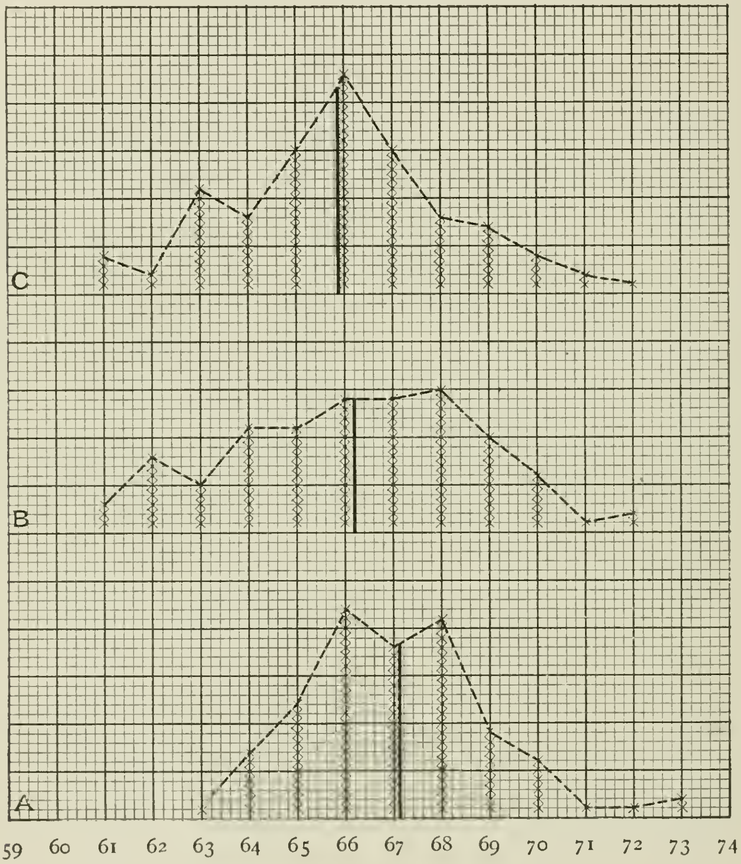

Fig. 1.

If we now tabulate the dorsal fin-rays of an equal number of flatfish from another locality, it is evident that if the fishes in both localities are alike, the curves will coincide. If they are different, even slightly so, the lack of coincidence will indicate the difference. The curve drawn at *B*, Fig. 1, is based on the enumeration of the dorsal fin-rays of 100 flatfish taken at Waquoit, Mass., from a small bay only eight miles east from Woods Holl. Compared with curve *A*, the Waquoit curve lies further to the left, has a longer base, and a less altitude. The Waquoit collection thus contains several fish, the number of dorsal fin-rays of which are less in number than those of fish taken at Woods Holl. The Waquoit fish are more variable, the amplitude at Woods Holl being from 62 to 72 (eleven points), while the amplitude at Waquoit is from 60 to 71 (twelve points). The depressed curve of distribution in the second curve is an indication of greater variability and general indifference to the "ideal mean." The arithmetical mean, represented by the vertical line, is 65.2, the Waquoit fishes averaging about one dorsal fin-ray less than the Woods Holl specimens.

Curve *C* represents the distribution of 100 flatfish from Bristol, R. I., from a body of water located about fifty miles west of Woods Holl. Compared with curve *A*, the Bristol curve lies further to the left and has a broader base, though its culminating point is very definitely indicated. The arithmetical mean is 64.9.

It is thus seen that there is a measurable difference between collections of fish from different localities, even though the fish *individually* present no perceptible difference.

There is correlated with the increase or decrease in the number of dorsal fin-rays, an increase and decrease in the number of anal fin-rays, as shown in Fig. 2. The Woods Holl specimens average a large number of dorsal and also a large number of anal fin-rays, 66.1 dorsals and 49.7 anals. The Waquoit specimens average a less number of dorsal fin-rays (65.2), and they also have a less number of anal fin-rays (48.6). The Bristol specimens average only 64.9 dorsal fin-rays and 48.7 anal fin-rays. The individuals also partake of this correlation, those having a larger number of dorsal fin-rays tending towards the possession of a larger number of anal fin-rays.

If it is proposed to test the result of re-stocking a locality in which a species of fish has become reduced in numbers, it is necessary to first determine the "curve of distribution" from

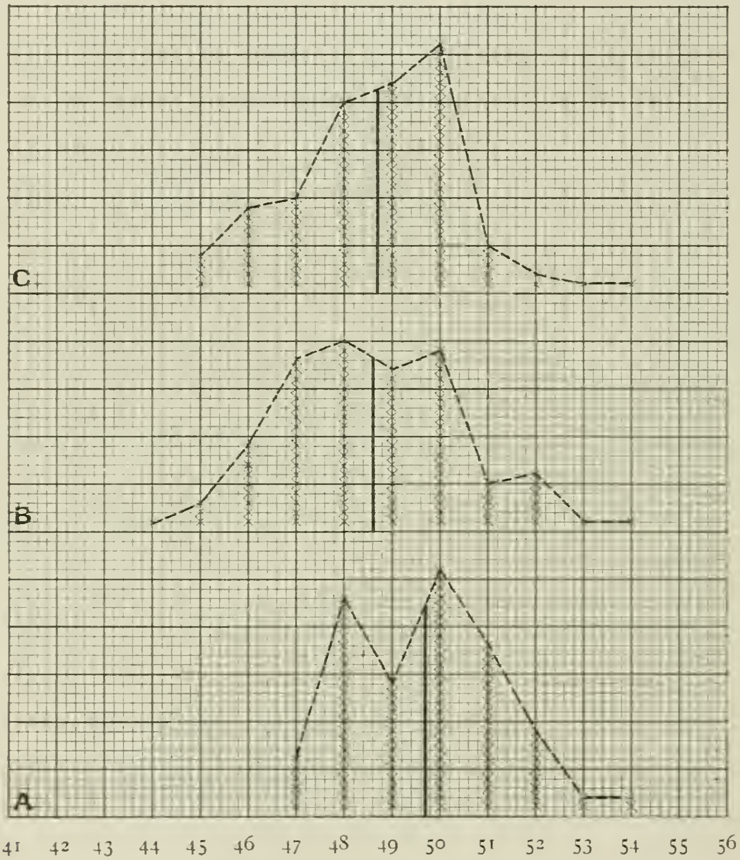

Fig. 2.

fish native to the locality, and this curve may be based on any measurable structural character, such as the number of fin-rays, the number of scale-rows, or the number of vertebræ. One must then determine the "curve of distribution," for the same structural character, of fishes of the same species, but abundantly found at another locality, from which the "brood fish" are to be taken. After the "planted fish" have had time to mature, new curves should be plotted for the first locality. If these curves are practically the same as those originally made, it is reasonable to conclude that the re-stocking has been ineffectual. If, however, the new curve approaches the curve of the locality from which the "brood fish" were taken, it is reasonable to conclude that the influence of the foreign specimens has been felt, and the re-stocking has been effectual.

The following objections may be raised to the above method:

(1) It may be that, due to the small number of specimens (100), the curve *A* is not characteristic of the Woods Holl specimens, and its difference from curve *B* is only accidental. To test this source of possible error I have examined three separate groups of flatfish, all from the same locality, each group containing 100 specimens. The resulting curves are strikingly alike. Of course it would be much more satisfactory to base all the curves on the enumeration of the fin-rays of one thousand rather than one hundred specimens, but even one hundred specimens yield fairly definite results, though the curves are somewhat uneven.

(2) It may be that the variation in the position of the curves is a result of age, *i.e.*, the fishes from Woods Holl averaged a larger number of fin-rays because they were somewhat older.

If there is an increase in the number of fin-rays on the part of the older specimens, this increase can be readily detected by simply comparing the average number of fin-rays of the younger with the average number of fin-rays of the older fish. Fifty-three young fishes, less than 10 inches in length, have a mathematical average of 66.1 dorsal fin-rays. Forty-seven older fishes from the same locality, all over 10 inches in length, average practically the same number of fin-rays, *i.e.*, 66.3. In this collection of 100 fishes, the fourteen smallest have a greater average number of fin-rays than the fourteen largest. There is then no material increase in the number of fin-rays with increase in age.

(3) It may be that the variations tabulated in Fig. 1 are the result of environmental conditions expressed upon the fry and young — acquired characters of questionable hereditary value;

i.e., it may be that the fry reared at Woods Holl would attain to a larger number of dorsal fin-rays than the *same* fry reared at Waquoit.

While certain experiments that the writer has made induce him to believe that these variations in the number of dorsal fin-rays may be deep-seated blastogenic characters, the influence of the environment, even if it should affect the ontogenic process, cannot vitiate the method, for if it is insisted that certain external influences may affect the fry *after* liberation from the hatchery, and the results of these influences are expressed by a change in the fin-ray formula, it must also be equally true that the more extreme and unusual environmental conditions imposed upon the still younger organism while *within* the hatchery, will leave their stamp also, and the artificially hatched fish will thus present some peculiarity, acquired though it may be, which will be brought out by the plotting of "curves of distribution."

THE BASAL SEGMENTS OF THE HEXAPOD LEG.

By L. B. WALTON.

American Naturalist, Vol. XXXIV, No. 400, April, 1900.

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THE BASAL SEGMENTS OF THE HEXAPOD LEG.

L. B. WALTON.

At the base of each leg in the Hexapoda are a series of segments and sclerites which enter into the composition and serve as a support of the appendage. These are the trochanter, *coxa genuina*, meron[1] trochantin, and antecoxal piece. The difficulties in the way of accounting for the origin of these segments and homologizing them in the various orders have caused morphologists more or less trouble.

By reason of the fusion which has taken place between the trochanter and femur in the Myriopoda and Hexapoda, many writers on insect anatomy hold that the trochanter is merely a portion of the femur which has in some manner become constricted so as to form an apparent but not an actual segment. The fusion, however, between the two parts is a specialization acquired during the later embryonic stages of development.[2] A similar case of ankylosis is often noticeable between certain segments of the appendages in Crustacea. Bordage[3] has advanced the theory, from observations based on certain Phasmidæ, that the two segments have become coalesced in the Arthropoda as a result of ecdysis. Since the same fusion, however, is very pronounced in the Myriopoda, particularly among the Diplopoda, where Verhoeff[4] believes the trochanter

---

[1] In order to distinguish between these two parts, which have been confused under the name "coxa," I have called the piece articulating with the trochanter *coxa genuina*, and the posterior lateral part articulating with the epimeron, meron (from *μηρός* = thigh), since its lateral margin is always found in articulation with the epimeron.

[2] The "two-jointed trochanter" of Hymenoptera [Terebrantia] appears to be a secondary modification, the lower part ["*apophysis*," Ratzeburg] being derived from the femur. This is the view held by Sharp, *Camb. Nat. Hist.*, vol. v, p. 520.

[3] On the Probable Mode of Formation of the Fusion between the Femur and Trochanter in Arthropoda. *Comptes Rendus de la Société de Biologie*, tome v, No. 28, pp. 839–842, 1898. Also *Ann.* and *Mag. Nat. Hist.*, vol. iii, pp. 159–162, 1899.

[4] Ein Beitrag zur Kenntniss der Glomeriden. 1895.

is in many cases entirely absent, it is evident that it is a characteristic of a primitive stem form, and has not arisen, as Bordage suggests, from an "ancestral form belonging to the existing Phasmids in which there was a distinct articulation between the two consecutive segments."[1] In addition to ecdysis, insisted upon by Bordage,[2] we must take into consideration various other selective factors, chief among which appear to have been mutilations by enemies. The severing of the segments, which resulted from either factor, would probably occur near the base of the appendage, and the favored forms would be those in which the two segments were approaching the fused condition, the invagination of the chitinous wall preventing undue hemorrhage. Autotomy, which Bordage so fully explains, would undoubtedly play an important part here. It also appears advantageous to poly-

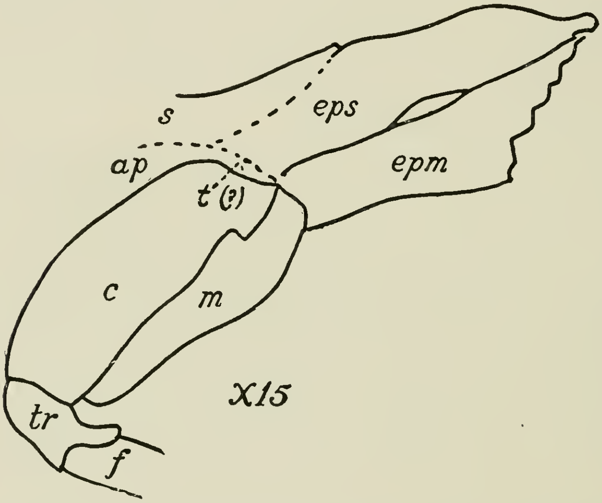

FIG. 1. — *Panorpa communis.* Metathorax; *c*, coxa genuina; *m*, meron; *eps*, episternum; *epm*, epimeron; *ap*, antecoxal piece; *s*, sternum; *t* (?), trochantin; *tr*, trochanter; *f*, femur.

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[1] I have adopted the translation as given by Austen.

[2] The position of Bordage in regard to the manner in which the fusion has come about is clearly on the side of Neo-Lamarckianism, since he attributes it to "a mechanical strain," and says that it is an "example of a character acquired by use . . . and then transmitted by heredity." This conclusion, however, as I have endeavored to show, seems unwarranted.

podial forms that a series of the appendages move more or less in unison, and it is obvious that such rhythmic motion is better maintained with the articulation of a coxa and trochanter alone than with an additional articulation between the trochanter and femur. This may be a factor in accounting for the more pronounced fusion of the two segments in the Diplopoda.

In 1893 Hansen[1] endeavored to homologize the trochanter of the Hexapoda with the ischiopodite in Crustacea. This homology was based on the supposition that the part assumed by him to be the trochantin[2] in the Cicadaria (Cicadidæ, Fulgoridæ, Cixidæ, etc.) was the homologue of the coxopodite in Crustacea. In referring to Machilis, he has considered the trochantin of the prothoracic coxa as a primary segment, homologous with the coxopodite. From comparisons, however, with both Chilopoda and Diplopoda, we would regard the trochantin rather as a specialized character of the Hexapoda, which is absent in the Crustacea. Homologies based upon the form of the segment and manner of articulation certainly appear ques-

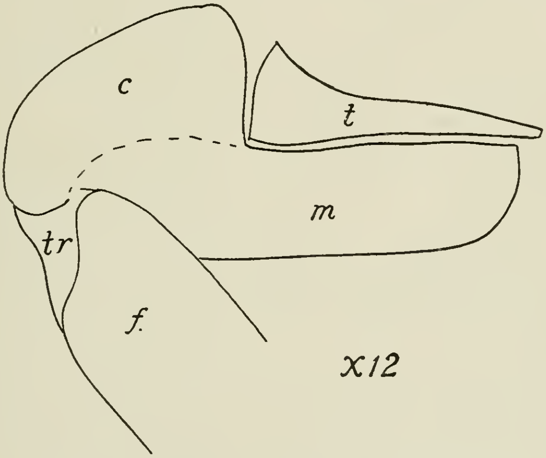

Fig. 2.—*Hydrophilus triangularis.* Mesothoracic coxa.

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[1] Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insecten. *Zool. Anz.*, pp. 193–198, 201–212, 1893.

[2] It seems probable that Hansen has here applied the name "trochantin" to the antecoxal piece and trochantin together.

tionable, since pronounced variations often occur within the limits of a single group.[1]

Until a closer relationship can be shown in the lines of descent of the two groups, Hexapoda and Crustacea, it would seem that an attempt to homologize the segments of the appendages would scarcely be justified. For the time being, we must assume that the segmentation of an appendage is a result brought about by certain indefinite factors, and that in these groups it does not necessarily imply a phylogenetic relationship.

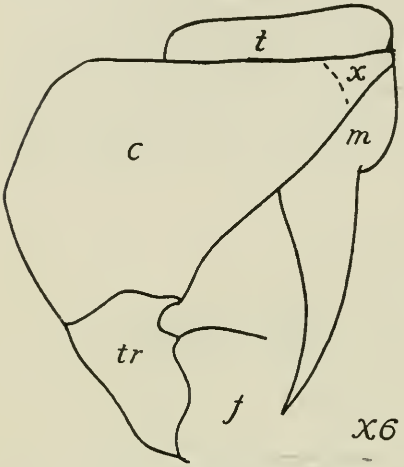

Fig. 3. — *Pomponia imperatoria.* Metathoracic coxa; *x*, area formed by development of coxal groove [Fig. 4 *c'*] and corresponding to lateral portion of *c*, Fig. 4.

That the trochanter of the Myriopoda and Hexapoda represents a distinct segment seems obvious, and that its fusion with the femur took place in some ancestral myriopod-like form appears probable.

Three sclerites, as a rule, enter into the composition of the segment to which the name coxa is given, *viz.*, *coxa genuina*, meron, and trochantin. Audouin[2] applied the name "trochantin"[3] to the lateral margin of the posterior coxa (meron) in *Dytiscus circumflexus*, erroneously believing it homologous with the trochantin on the anterior and mesal coxæ[4] of *Buprestis*

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[1] Compare Arachnida, or, in Coleoptera, the metathoracic coxa of Dytiscus and Hydrophilus.

[2] Recherches anatomiques sur le thorax des animaux articules et celui des insectes hexapodes en particulier. *Ann. Sci. Nat.*, tome i, p. 125, 1824.

[3] This word had been previously used by Chaussier [Littré, *Dict. de Médecine*, p. 1632] during the latter part of the eighteenth century to designate a small process on the upper part of the femur in the human skeleton. From the note Audouin appends, he evidently felt some constraint in conforming to the custom of transferring such terms to invertebrate anatomy when no homologies could be demonstrated.

[4] In the metathorax of the Coleoptera the trochantin has been lost through specialization, although traces of it are noticeable among many forms (Hydrophilus, certain Cerambycidæ, etc.).

gigas, which he subsequently mentions.[1] Later, in his contribution to Cuvier's "Le Regne Animal," he figures the prothoracic trochantin of *Oryctes nasicornis*. The present confused terminology of these segments is due to the preceding error of Audouin. Newport[2] made a somewhat similar error by describing the anterior margin of the coxa (*coxa genuina*) in *Hydrous piceus*, as the metathoracic trochantin. Among the recent writers on insect anatomy, Packard[3] confuses the trochantin with the meron; Miall and Denny[5] hold that the occurrence of the joint applied to the coxa (trochantin) "is so partial" that it need scarcely be taken into consideration; Sharp[4] believes with Packard that the posterior part of the coxa (meron) in Panorpa represents the trochantin; while Comstock,[6] in a description of the metathorax in *Euchromia gigantea*, agrees essentially with the preceding, although he correctly figures the trochantin of the prothorax and mesothorax. Lowne[7] regards the piece

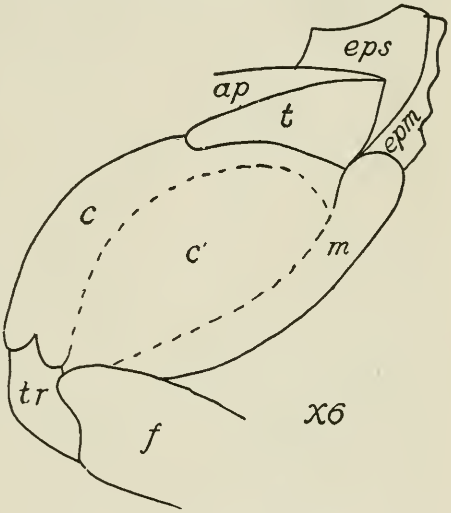

Fig. 4.—*Periplaneta orientalis*. Metathorax; *c'*, coxal groove formed for reception of femur.

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[1] Étude de la poitrine ou des pattes inférieures et latérales du mesothorax. *Ann. Sci. Nat.*, tome i, p. 426, 1824. This is merely a continuation of Recherches anatomiques.

[2] Todd's *Cyclopedia of Anatomy and Physiology*, p. 916, 1835–59.

[3] Systematic Position of the Orthoptera in Relation to the Orders of Insects. *Third Report U.S. Ent. Com.*, 1880–82. *A Text-Book of Entomology*, p. 95, 1898.

[4] The Structure and Life History of the Cockroach, p. 61, 1886.

[5] *Camb. Nat. Hist.*, vol. v, p. 104, 1895.

[6] Manual for the Study of Insects, p. 504, 1895. It was due to Professor Comstock's suggestion of a possible error in considering the lateral margin of the metathoracic coxa of Euchromia as the actual homologue of the mesothoracic trochantin, that the study leading to this paper was commenced.

[7] The Anatomy, Physiology, Morphology, and Development of the Blow-Fly, vol. i, p. 179, 1890–92.

termed by him "epitrochlea"[1] as "certainly the trochantin of Audouin," ignoring his previous suggestion that one should adhere to the rule of priority. Several other writers, notably Latzel (Chilopoda), Comstock and Kellogg (Lepidoptera), and Kolbe (Lepidoptera, Trichoptera, and Panorpa), have mentioned the existence of an apparent suture in the coxa of certain groups under consideration, but without attempting to discuss its meaning.

Immediately in front of the metathoracic coxa, particularly among the Coleoptera, a small sclerite is discernible, which bears the name of antecoxal piece. This is also well shown in Cicada, some species of which (*Cicada dorsata*) possess a piece homologous with that found in the Coleoptera; while in others (*Cicada tibicen*),[2] instead of being chitinized, the part is often membranaceous in structure, and serves to retain the coxa more firmly in the coxal cavities, thus indicating its origin; and the presence of a homologous piece in the mesothorax of many Coleoptera (Passalus, etc.), occurring at the same time with the trochantin, proves that it is distinct from the latter.

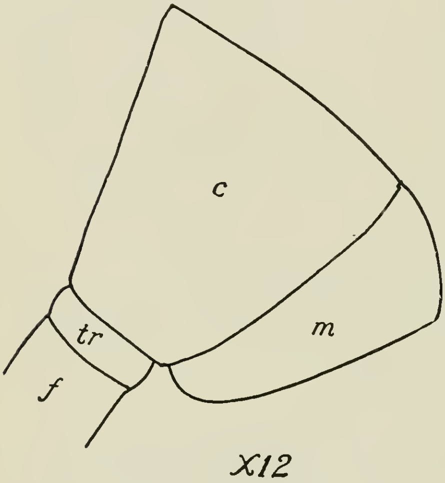

FIG. 5.—*Scutigera sp.* Coxa showing fusion of coxa genuina and meron.

The *origin* of the three pieces, *coxa genuina*, meron, and trochantin, the relative positions of which are shown in the accompanying figures, is more difficult of explanation. A striking characteristic of the Hexapoda and Chilopoda is the more or less complete fusion of the first two (*coxa genuina* and

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[1] The homology of this with the trochantin appears doubtful.

[2] Although a good series was examined in which the other sclerites were well chitinized, the absence of chitinization in the antecoxal piece may be the result of immaturity. This, however, would not alter the conclusion.

meron) into the so-called coxa. Theoretically the episternum[1] and epimeron may be regarded as corresponding basal segments of these fused pieces, and taking into consideration the apparent absence of a piece homologous with the meron in the Diplopoda, we are led to the interesting inference that this group represents a class in which *each primitive metamere bears a pair of appendages*, while the Chilopoda and Hexapoda represent a widely divergent class, in which *two primitive metameres have attained a more complete fusion*,[2] *the rudimentary appendage belonging to each posterior segment fusing with the base of the functional appendage belonging to the anterior metamere*.[3] The posterior appendage would then be represented by the meron and epimeron.[4] In this case we can refer the origin of *coxa genuina* and episternum, as well as the meron and epimeron, to the same causes which produce segmentation in the appendage. The trochantin appears to be nothing more than a part of the antecoxal piece, a lateral prolongation of which became constricted off in a primitive form. Again we are confronted with the question as to the origin of the appendages in the Arthropoda, whether they are ventral or dorsal parapodia, or a fusion of the two, as in Nereis, or whether the

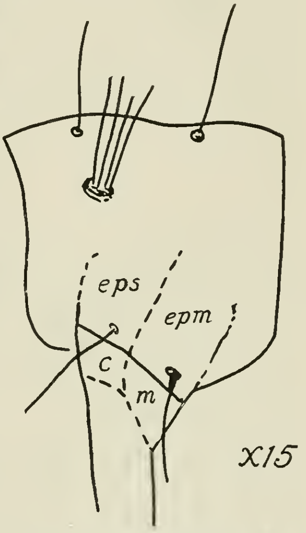

Fig. 6. — Larva of *Phryganea*. Mesothorax, showing early indications of coxa genuina and episternum fusing with meron and epimeron.

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[1] Frequently the episternum appears to be cut off from the coxa by the sternum or by the trochantin, but in such cases the coxa is usually prolonged internally, so that it meets the episternum.

[2] At present there appears to be better evidence for believing that these pieces indicate a fusion of the segments than to hold that an exopodite and entopodite are represented.

[3] A study of the position and homologies of certain of the pleural and dorsal sclerites in Hexapoda and Chilopoda appears to confirm this inference.

[4] While thus far the majority of embryological evidence appears to be against this view, it seems possible that secondary modifications have caused a misinterpretation of the lines of descent.

origin was entirely independent of the parapodia. A study of Peripatus appears to throw no light on the subject under discussion, beyond indicating that in using the term "primitive metamere" we must not exclude the idea that such a metamere may in turn represent a fusion of an indefinite number of annuli. Evidence is thus added to a segment-fusion theory rather than to the biramose theory.

While it appears possible that the exopodite and entopodite in Crustacea may have developed from dorsal and ventral parapodia, in direct contrast to the manner indicated above for the Chilopoda and Hexapoda, further study may show a common origin of the two processes.

SUMMARY.

In Hexapoda and Chilopoda the "coxa" is composed of two more or less fused segments, *coxa genuina* and meron.

The antecoxal piece results from the chitinization of the membrane connecting the coxa with the sternum.

The trochantin probably originated from a lateral portion of the same membrane.

Audouin erroneously homologized the lateral margin of the posterior coxa in *Dytiscus circumflexus* with the trochantin of the prothorax and mesothorax.

The trochanter represents a distinct segment of the legs.

The meron and *coxa genuina*, together with their corresponding basal segments epimeron and episternum, give evidence of a fusion between two primary metameres in the Hexapoda and Chilopoda.

In Hexapoda and Chilopoda the anterior metamere bears the functional, and the posterior, the rudimentary leg.

Of the primitive Hexapoda, Neuroptera [Planipennia] exhibit the most generalized condition in the development of the coxa, while in Thysanura and Orthoptera a high degree of specialization is shown.

ANATOMICAL LABORATORY, BROWN UNIVERSITY.
October 27, 1899.

THE WORK AT THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION AT WOODS HOLL.

By H. C. BUMPUS.

Science, N. S., Vol. VIII, No 186, July 22, 1898.

[*Reprinted from* SCIENCE, *N. S., Vol. VIII., No. 186, Page 96, July 22, 1898*].

THE WORK AT THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION AT WOODS HOLL.

THREE months ago the United States Fish Commission announced that its Biological Laboratory would be reopened; that it would be equipped for investigation; that men of science would be welcome, and that every effort would be made to collect all needed material, and to furnish, within certain limits, all necessary instruments and apparatus for research. The Station is the most extensive plant for the study of marine life and practical fish-culture in the world. There are four buildings: The Hatchery, Laboratory and Aquarium; the Residence; the Shops and Store House; and the Power House. It is in possession of a small fleet of steam and sailing vessels, and by special enactment the officers are empowered to use, at their discretion, any means for the capture of fish or other marine organisms.

The Commission has refurnished the Biological Laboratory and added ten new rooms for research. It has equipped a laboratory for physiology. It has purchased a bacteriological outfit, and a creditable library of biology and fish-culture has been installed. Two steam launches and the schooner Grampus have been attached to the Station, several fine-mesh seines, trawls and tow-nets have been purchased, and a large fish-trap has been placed at a favorable locality.

From the day of the opening of the laboratory, April 1st, several tables have been continuously occupied, and, at the present time, the scientific force numbers twenty-four. Several have expressed the desire of extending their work during the autumn and winter months, and it is proposed to keep the laboratory open throughout the year.

The Commission does not attempt to instruct or to dictate as to what lines of research are to be pursued, how the work shall be carried on, or where the results shall be published. It is convinced that all lines of biological research are indirectly, if not also directly, helpful to its more immediately practical work, and it happens that fully one-half of the investigators are now busy with problems bearing directly upon the anatomy, embryology, physiology and pathology of fish. The large corps of collaborators has made it possible to secure definite data respecting the breeding habits of many marine forms. The floating-fauna has been systematically examined; valuable information has been gained respecting the larval life of the star-fish, the developmental stages of the clam, the rate of growth of the scallops, the causes of mortality of lobster fry, and the pathogenic bacteria infesting fish.

With the cooperation of the Marine Biological Laboratory, it is proposed to make a series of synchronous observations on the temperature and floating fauna of Vineyard Sound. The combined vessels of the two laboratories provide a sufficiently large fleet to make these observations of special interest. It is also proposed to resume again the deep-sea work begun by the Commission many years ago, though the temporary use of the Fish Hawk by the United States navy will prevent the work from being undertaken the present season.

H. C. Bumpus.

THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTH OF MARCH, 1898.

By H. C. BUMPUS.

Science, N. S., Vol. VII, No. 171, April 8, 1898.

[*Reprinted from* SCIENCE, *N. S., Vol. VII., No. 171, Pages 485–487, April 8, 1898.*]

THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTH OF MARCH, 1898.

THROUGH the courtesy of the United States Commissioner of Fish and Fisheries, several naturalists have been enabled to make use of the equipment of the Biological Station at Woods Holl during the past month, and the following notes may be of interest to those who contemplate pursuing lines of investigation at either of the marine laboratories:

The water has swarmed with animal life, and many forms rarely or never captured during the warmer months have been found in abundance. Breeding animals have yielded rare embryological material, and all forms of life have had great vitality, due probably to the low temperature of the water. The temperature of the water has ranged from 38 F. at the beginning of the month to 43 F. on the 30th. Its specific gravity has varied from 1.0232 to 1.0236.

Among vertebrates the winter flatfish (*P. americanus*) has been taken in large numbers, and spawning individuals have yielded an abundance of embryos and young. The clustered eggs of the small sculpin (*Acanthocottus æneus*) have been taken from nets and from sea-weed, and the young have been conspicuous in the *Auftrieb*. The surface towings have also yielded young of the common cod (A. *callarias*), eggs of which were hatched at the Station during the earlier portions of the month. Young cod, from one-half to three-fourths of an inch in length, have been found feeding exclusively upon Copepods, and associated with them were the somewhat larger pollock (*Pollachius virens*). The Gadidæ have also been represented by numerous adult 'frostfish' (*Microgadus tomcod*), though the breeding period of this species is in December. The young of the sand-launce (*Ammodytes americanus*), from one-half to one inch in length, and of the eel (*A. chrysypa*), from two to two and one-half inches in length, have also been taken. The pipe-fish (*Siphostoma fuscum*) was not examined, though it was found in Narragansett Bay with eggs and with young March 22, 1897.

The 'alewife' or spring herring (*Pomolobus pseudoharengus*) has begun to enter the fresh-water streams from the sea, though it has not yet begun to deposit its eggs.

Several Crustacea are already breeding. The green crab (*Carcinus granulatus*) is carrying about its orange-colored clusters, and Mysis has its brood-pouches distended with embryos. Several species of Amphipods bear eggs. One of these is a large light-colored species, apparently in the height of its breeding season; thousands have been captured in small traps baited with fish. Associated with this amphipod and captured in the same manner, though not breeding, were numerous examples of the Isopod, *Cirolana concharum.* Enormous, bright-colored Caprellas were dredged in the 'Sound,' and many eggs were taken. *Crangon vulgaris* is breeding, of course, and it would be interesting to learn when this species is not pregnant. *Palæmonetes vulgaris, Virbius zostericola* and *Hippolyte pusiola* have been frequently taken, the latter with eggs. The Eupagurids (*E. Bernhardus*, *E. longicarpus*, *E. policaris* and *E. annulipes*), though showing enlarged ovaries through their transparent body-walls, have not extruded their eggs. The same may be said of *Gebia affinis* and *Callianassa stimpsoni*, many individuals of which were taken in Narragansett Bay on March 8th, of the present year.

Limulus has not yet approached the shore, though a single specimen was taken in a fyke-net at Waquoit on March 25th. No Cirriped larvæ have been taken. On January 3, 16 and 22, 1896, great numbers of these nauplii were taken at Bristol Narrows, R. I., and on February 14th they were still common, though not so abundant. Of course, Copepods have formed a large proportion of the organisms taken at the surface, and they appear to be even more abundant than during the summer months. Volumetric data respecting the Plankton are much desired, though the efficiency of the ordinary methods for securing Plankton will be materially affected by the annoying presence of a gelatinous alga, which quickly renders the net all but useless.

Vermes.—Having seen myriads of *Nereis virens* swimming in the shallow water of the shores of Narragansett Bay, and having collected several hundred specimens on March 23, 1897, when the water was actually colored with the extruded eggs and spermatozoa, we were not surprised to find several individuals swimming about at Woods Holl. The eggs of this species have not been carefully studied, though they offer some interesting features to those at work upon cell-lineage. Specimens of immature eggs were taken on January 29, 1896, and at Bristol Narrows on March 26th of the same year there were scores of 'spent' males. The height of the breeding season, then, is probably during the earlier and middle portions of the month of March. Annelid larvæ of other species have been abundantly taken both in January and in February.

Heteronereis limbata was found at Woods Holl, swimming about on the surface, in broad daylight. The males, on examination, proved ripe. *Autolytus cornutus* was frequently taken with eggs, and *Harmothœ* and *Lepidonotus* appeared to be almost ripe. *Chœtopterus*, *Rhynchobolus*, *Maldane*, *Sthenelais*, *Trophonia*, *Clymenella*, and *Phascolosoma* were collected, but not in sufficient numbers to definitely determine their sexual condition. *Sagitta* was excessively abundant, and the large clear eggs could easily be seen through the transparent integument.

Mollusca. — Cephalopod mollusks have not arrived, and time has not permitted the examination of the Lamellibranchs. The egg-capsules of the smaller Gastropods, so abundant later in the season, were conspicuous by their absence. Naked mollusks of gorgeous coloring were dredged in the 'hole' and 'sound.' *Doto coronata, Eolis bostoniensis* and *Alderia harvardiensis* were the most abundant species ; the two latter are breeding in the laboratory.

Echinoderms.—There is every indication that April will be an excellent time for one who wishes to secure an abundance of Echinoderm material, either for embryological or for experimental study. The star-fish are approaching sexual maturity. The most attractive eggs are those of the 'sand-dollars' (*Echinarachnius parma*). Bushels of this echinoid were dredged off Quick's Hole. The eggs readily fertilize and develop normally. The first cleavage occurred two hours after fertilization; the gastrulation occurred in from 30 to 36 hours. 'Plutei' from embryos hatched on March 22d were raised without difficulty, and are now, at the end of the month, still living. I regret that observations on the breeding habits of the Holothurians were not made.

Cœlenterates.—The wealth of Cœlentarete life found during this month is bewildering and distracting. Ctenopores (adult *Mnemiopsis* and *Pleurobrachia*) hydro- and scyphomedusæ abound. The *Ephyra* and young of *Aurelia* were taken at Waquoit in countless numbers and lived in the laboratory from the 16th to the close of the month. On March 30th the calm surface of the water in Great Harbor was literally spangled with the slightly protruding discs of *Cyanea*. The piles and rock-work of the 'basin' are covered with breeding 'Hydroids' of *Coryne*, *Clava* and *Parypha*. The dredge has brought up *Sertularia argentea*, laden with eggs, and, most beautiful of all, enormous specimens of *Tubularia couthouyi*. The expended hydranths of this species are as large as 'bachelor's buttons,' and are borne upon a stalk several inches in height. They literally droop with their burden of ripe gonophores. The young are possessed of remarkable vitality and would make excellent material for experimental work. *Tima formosa*, though abundant in Narragansett Bay from January to March in 1896, has not thus far been seen either in the

'Sound' or in Buzzards Bay. *Metridium*, *Sagartia*, *Halcampa* and *Astrangia* have been taken, though an examination of their reproductive glands has not been made. *Grantia* is not abundant, and the individuals collected were small and apparently immature.

H. C. Bumpus.

THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTH OF APRIL, 1898.

By A. D. MEAD.

Science, N. S., Vol. VII, No. 177, May 20, 1898.

[*Reprinted from* SCIENCE, *N. S., Vol. VII., No. 177, Pages 702–704, May 20, 1898*].

THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTH OF APRIL, 1898.

THE temperature of the water has remained above the average almost throughout the month. During the first week the thermometer registered 41 F. to 42 F.; dure ing the last week, 45 F. to 46 F. The specific gravity has varied from 1.0231 to 1.0235. The weather has been generally cloudy and the temperature of the atmosphere low.

Vertebrates. — The winter flatfish, *P. americanus*, ceased spawning early in the month, and, though the height of the breeding season was in March, few of the young flatfish have been taken, even over the natural spawning grounds. Young sculpin (*A. œneus*) were very abundant in the tow, especially during the first of the month. On April 4th a very large number were captured, and many were taken on the 18th. On the 27th a few more were taken which apparently had just hatched. Small cod and pollock have been frequently captured, and the latter were more numerous than in March. The young of the sand-launce (*A. americanus*) have diminished in numbers but little since last month, though some have increased considerably in size. On the 17th an unusually large number were taken. The young of the fall herring (*A. harengus*), from three-fourths of an inch to three inches in length, have appeared in increasing numbers. A few specimens of

Ctenolabrus were examined on April 19th, but the sexual glands, though quite large, were not nearly mature. *Petromyzon* has been taken in the fish traps, and may be seen frequently in the markets.

Crustacea.—The small species of *Gammarus*, abundant in the tow during March, are still breeding. Their appearance, from day to day, is uncertain. One day there may be only four or five in the net, and the next day hundreds may be captured. A small species of *Mysis*, about one-half inch in length, has been abundant, and the brood-pouches have been filled with eggs or embryos. A larger species, bearing well developed embryos, was abundantly taken during the first two or three weeks. The red copepod, the favorite food of the young cod, sculpin and sand launce, has been present in great numbers. A few were caught at every haul of the skimming-net, and frequently great numbers were taken. Their sudden appearance and disappearance is very puzzling. Dr. Loeb has shown that in the aquaria they are positively or negatively heliotropic, according to the temperature, but I find that when first transferred from the surface-net into a dish a large minority become negatively heliotropic, though, of course, all are subjected to temperature of the ocean. Many other species of copepods were caught, though not in great abundance. Some were bearing eggs attached to the abdominal appendages. A small parasitic copepod is very frequently found attached to the young cod, sand launce and sculpin. Perhaps one-third of these fish are thus infested. The *isopod* (*Cirolana concharum*) was not breeding on April 26th, and the associated *amphipod* had apparently passed its breeding season. *Hippa* has not begun to lay, though the ovaries are full of large brilliantly-colored eggs. They have been found breeding in July.

Vermes.—No *Nereis virens* or *Nereis limbata* have been seen at the surface. *Autolytus*, with egg-clusters attached, were regularly taken in the tow, usually three or four at a time, during the earlier portions of the month. Later in the month only a few were noticed. An interesting species of *Syllis* has been taken from among the hydroids and algæ on several occasions. These annelids are in almost every case about to undergo fission. The new head is found in all stages of development in the midst of the trunk metameres. The eyes on the new head are large and brown, while those on the first segment are small and black. These annelids are full of mature eggs, which, in some instances at least, occupy the body-cavity both in front of and behind the new head. A light, cream-colored terebellid, full of eggs, has been taken from time to time, and was also taken during March. It is almost invariably present in clusters of the hydroid *Parypha*, along with one or two species of *Caprella*, *Eolis* and the little gasterpod *Astyris*. *Harmothoe* sp. has commonly been found under stones and among hydroids, laden with beautiful pink eggs, which show clearly through the body-wall. On April 11th the eggs, teased from the body cavity, were easily fertilized, and in less than two hours some had reached the eight-cell stage; specimens taken April 17th were also full of eggs. The common *Lepidonotus* has been laying during the last two weeks. *Cirratulus grandis*, collected at Ram Island, April 9th, and at Pine Island, April 17th, contained great numbers of eggs, apparently nearly ripe, though an attempt at artificial fertilization was not successful. Some of the spermatozoa were motile, but the male worms did not have the bright orange color which characterizes them in the height of the breeding season, early in July. Sagitta, though numerous, has been less abundant than in March. The specimens are much larger than those found during the summer months, and are filled with eggs. During the last week there has been a notable decrease in their numbers, and small individuals, less than one-half inch in length, have been frequently noted.

Mollusks.—A few egg-strings of *Sycotypus* and *Fulgar*, containing well-formed shells, have been taken at various localities along the shore. *Urosalpinx* has not begun to breed. Young 'veligers' of *Crepidula fornicata* were found in the egg-packets on April 6th and on April 17th, though specimens with young are not frequent. The eggs of a small gasteropod abounded on the stems of *Parypha* during the entire month. Five species of nudibranchs, belonging to the genus *Eolis*, have laid their eggs in the aquaria. The hermaphrodite gland of *Eolis papillosa* contains giant erythrophilous spermatozoa, like those of *Paludina vivipara*, which Auerbach has described. Eggs of *Ilyanassa* were found April 25th and 27th. The 'sand collars' of Natica were found at Hadley Harbor, April 25th.

Echinoderms.—*Echinorachnius parma* has not been examined since the early part of the month, when it was breeding abundantly. On April 16th the plutei, developed from eggs fertilized on March 22d, were still living in the aquaria. Eggs of this species have also been obtained in June and July. It is a remarkable fact that, though neither *Asterias vulgaris* nor *Asterias forbesii* at Woods Holl contain ripe sexual products, those of the latter species in certain parts of Narragansett Bay have been full, almost to bursting, of eggs and spermatozoa since the early part of April. The holothurians *Thyone*, *Leptosynapta giradii* and *L. roseola*, were examined April 24th, and were all full of nearly ripe eggs or sperm. Not the least attractive of the echinoderm eggs are those of the little starfish, *Cribrella sanguinolenta*. This species is not uncommon at Woods Holl, and the eggs, which were frequently laid in the aquaria during the third week in April, are as large as those of *Clepsine* or *Sycotypus*. They develop slowly, reaching the two-cell stage in about 6 hours. This material would undoubtedly be of great value in solving problems of cleavage and of echinoderm metamorphosis.

Cœlenterates.—The profusion of cœlenterate material was a feature of every collecting excursion during the first half of the ounth. Hydromedusæ of many different species were abundant in the tow until about the 17th of the month, and since then have been caught in small numbers. Among these, *Hybocodon* was perhaps the most numerous, although *Coryne* and *Tiaropsis* has been taken frequently. *Tima formosa*, abundant in 1897 at Newport, has not been seen. Hydroids of the brilliantly colored *Coryne* occurred in colonies that could be measured by the square yard, and those of a species of *Campanularia* could be measured by the square rod. On April 26th the *Coryne* had disintegrated. The large jellyfish, *Cyanea arctica*, has been represented throughout the month by specimens ranging from one-half inch to seven and eight inches in diameter, and *Ephyræ* were caught as late as the 21st. On April 8th the water at Waquoit was full of *Aurelia*, most of the specimens being from one to two inches in diameter, though some were much larger. *Metridium marginatum* was examined on the 18th, and was found to be full of eggs, apparently nearly mature. One of the 'sulphur sponges' was observed to extrude clouds of spermatozoa on April 10th.

The gelatinous alga, so abundant during March and the first half of April, gradually diminished in quantity after the 17th, and on April 25 little or none was found in the nets.*

A. D. MEAD.

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* The Breeding of Animals at Woods Holl for the month of March was published in 'SCIENCE,' April 8, 1898.

THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTH OF MAY, 1898.

By H. C. BUMPUS.

Science, N. S., Vol. VIII, No. 185, July 15, 1898.

[*Reprinted from* SCIENCE, *N. S., Vol. VIII., No. 185, Pages 58–61, July 15, 1898*].

THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTH OF MAY, 1898.

THE opening of the Biological Laboratory of the United States Fish Commission made it possible for a number of naturalists to work at Woods Holl during the month of May, and it is hoped that the abundance of animal life may attract others to the shore in 1899.

The temperature of the water during the month of May rapidly rose from 46 to 57 F. To this remarkable physical change both the fauna and flora responded, and the biological facies were materially altered.

Vertebrates.—The winter forms gradually disappeared and the familiar types of the warmer months began to arrive. The lampreys (*Petromyzon marinus*), ripe with eggs, were taken during the latter part of the month at East Taunton. Spiny dogfish (*Squalus acanthias*) were taken in Vineyard Sound, and *Raja ocellata* was abundant throughout the month, though probably not breeding. The transparent young of the common eel were frequently taken on the surface and in the shallow water. The fishermen say that the adults descend the streams while the alewives are passing up. This migration to the sea happens about the 12th, when there is the heaviest run, although many may be taken on subsequent nights. If the sky is clear and cloudless the catch is never so large as when dark and stormy. Late in the month several barrels of menhaden (*Brevoortia tyrannus*) were taken at Cuttyhunk, while throughout the month the skimming-net caught multitudes of young herring (*Clupea harengus*). *Fundulus heteroclitus*, ripe with eggs, was captured in great numbers at Falmouth on the 13th, where were also found two species of stickleback (*Gasterosteus bispinosus* and *Apeltes quadracus*), both sexually mature. An abundance of breeding pipe-fish (*Siphostoma fuscum*) were seined from eel-grass on May 13th, and they have been found, with pouches filled with eggs, as late as July 13th. The first mackerel (*Scomber scombrus*) was taken on May 3rd. A few butter-fish (*Rhombus triacanthus*) were taken in a trap at Cuttyhunk on the 11th, though reported at West Dennis on the 5th. They spawn in June.

Among the Serranidæ, *Roccus lineatus* usually arrives in May, although the present year we did not secure specific data. The white perch (*Morone americana*) spawns during this and the following month, and the sea-bass (*Centropristes striatus*), first seen on the 10th, was taken in large numbers on the 12th. It spawns in June. The scup (*Stenotomus chrysops*) were abundant at Cuttyhunk on the 11th, when thirty barrels were taken. It is said to spawn early in June. The squeteague (*Cynoscion regalis*), first taken in April, was occasionally brought to the station in May. The puffers (*Spheroides maculatus*) appeared during the latter part of the month, and a fine lumpfish (*Cyclopterus lumpus*) was also captured. The latter is said to breed in April. The Gurnards were represented by both *Prionotus carolinus* and *Prionotus strigatus*. It is estimated that there were at least one thousand in the trap on the 13th. Specimens examined on the 16th were not ripe, though the ovaries were large.

The Gadidæ abounded. Beautiful great pollock were almost daily brought to the laboratory; cod were so numerous that they found no market, and white hake (*Phycis tenuis*) were a positive annoyance to the fishermen. When so many inland laboratories are inadequately provided with animals for dissection it seems a great pity that hundreds of barrels of this beautiful material should yearly go to waste.

Among the Pleuronectidæ the summer flounder (*Paralichthys dentatus*) was often taken. The four-spotted flounder (*Paralichthys oblongus*) and the window-pane (*Bothus maculatus*) were abundant. Eggs of the four-spotted flounder were ripe in May, and have been hatched in the Chester jars. The period of incubation is about eight days. The eggs of the window-pane are of about the same size as those of *P. oblongus* and readily fertilize. The good eggs soon rise to the surface, leaving the immature and injured eggs at the bottom. The sole (*Achirus fasciatus*) was apparently ripe the latter part of the month. *Lophius* was abundantly taken from the 'Sound' traps on the shore of Marthas Vineyard.

Molgula and *Ciona* were ripe throughout the month.

Crustacea.—*Gammarus annulatus* occurred in swarms. The tow-net at one haul, on the 16th, contained over two quarts, and the animals were so numerous that in places they gave a distinct color to the water. Many had eggs. On the 23d they were only occasionally found. *Orchestia agilis* bears eggs in May, and is, of course, abundant. When *Cyanea* comes to Woods Holl in May, it is often accompanied by *Hyperia*; the crustacean bears at this time most beautiful great eggs, almost perfectly transparent. On May 6, 1892, many were collected at Woods Holl, and on June 8, 1893, they were abundant in Narragansett Bay. *Idotea* was found at Nahant with eggs, May 20, 1893.

Schizopods, adults laden with eggs and young, were daily taken. Lobsters began to hatch on the 16th, and thousands were planted in Vineyard Sound during the latter part of the month. *Crangon* was often heavy with young, though *Palæmonetes* did not deposit its eggs until the latter part of the month. *Eupagurus longicarpus* was found bearing well-developed eggs on May 9, 1890, and on May 16th the eyes of the embryos could be seen. *Carcinus granulatus* often had eggs, as did *Gelasimus* and *Libinia*. The crabzœa were first taken in the skimmings on the 10th, and were abundant on the 11th. *Hippa*, though often taken, was without eggs. Pairs of *Limuli* might have been collected by the hundred.

Vermes.—The tow-net brought in many surface forms. On the 7th *Autolytus* was taken, but without eggs. On the 10th several egg-bearing individuals were noted, and on the 11th Dr. Mead saw a male swim about like an excited *Nereis limbata* and finally fasten to one of the females with his jaw. Throughout the latter portion of the month *Autolytus* was taken in abundance. On May 17th swarms of Terebellids were observed to migrate from the clusters of *Parypha*, brought to the laboratory from Quick's Hole, and to gather on the sides of the aquaria. *Lepidonotus* bred throughout the first half of the month, and ripe females have been found as early as April 25th. Dr. Mead informs me that if the females are captured during the day they will deposit their eggs at about 6 p. m. The ripe females are generally greenish drab on the lower side, while the males are pinkish white. If the stagnant water, in which the animals have been retained during the day, is replaced by fresh sea-water the eggs or sperm will be seen to leave the nephridial openings of the posterior two-thirds of the body in streams. Since the eggs after fertilization settle to the bottom, the water may be renewed without difficulty. The embryos swim in from eight to ten hours and the gastrula stage is reached in about twenty hours. *Harmothœ*, found in the same localities as *Lepidonotus*, from which it is distinguished by having eighteen rather than twelve pairs of scales, breeds about one week earlier. The eggs may be secured and fertilized in the same way as those of *Lepidonotus*. The ripe females are bright pink on the lower side.

Dr. Mead found *Scolecolepis viridis* and *Clymenella torquata* breeding during the early part of May. The eggs of the former species are found in the sand-tubes; those of the latter are very large, but difficult to secure because of the shortness of the breeding season. Specimens absolutely ripe extrude the eggs in confinement, but if not absolutely ripe the eggs degenerate without being extruded. *Nereis limbata* was found swimming on the surface on the 13th. *Spirorbis* breeds during May, and the fully formed embryos may be shaken from the *Fucus*, to which the adults are attached. Fine large egg-bearing specimens of *Sagitta* were abundant until the middle of the month.

Dr. E. G. Gardiner reports that the small accœlous planarian, *Polychœrus caudatus*, was repeatedly found, that several examples of a large species of *Monotus*, collected near the Laboratory, laid thousands of eggs upon the walls of the glass jars in which they were confined, and that *Plagiostomum* freely laid in captivity. He also found great numbers of *Dinophilus*.

Mollusks.—The squid (*Loligo pealii*) made their appearance on May 7th, when several hundred were taken at Hadley Harbor. Many eggs in early stages of development were found, and the animals occasionally laid in the aquaria. Artificial fertilization is easily accomplished. Many squid were taken throughout the month, and one egg-mass found attached to a fish trap filled a large bucket. *Urosalpinx* was found breeding on the 21st. The sand-collars of *Lunatia* were frequently brought into the Laboratory, and naked mollusks often deposited their eggs in the aquaria.

Echinoderms.—On May 10th *Echinarachnius parma* showed no sign of exhaustion; larvæ of *Cribrella* were taken in the townet, and the Ophiurans, abundant at North Falmouth, contained only immature eggs. An earlier note, made at Nahant, reports *Ophiopholis* as ripe May 20, 1893.

Cœlenterates.—*Pleurobrachia rhododactyla* was not abundant. The reproductive elements were found to be ripe by Dr. McMurrich towards the end of May, 1890. *Berœ* was taken at Newport, R. I., on May 7, 1896, and at Bristol, R. I., on May 15th. *Mnemiopsis* and *Cyanea arctica* were only occasionally found. The planulæ of the latter may be easily raised in the Laboratory. They attach themselves in from seven to ten days after the eggs have left the parent. A few *Aurelia* of medium size were taken on the 7th, and again on the 16th, 17th, 18th and 19th.

On May 10th a few small specimens of *Tubularia couthouii* were dredged at Quick's Hole, and the large stems of specimens dredged on the 17th seemed to show signs of regenerative processes. On the 11th hydromedusæ were hatched from hydroids of *Obelia*, and on the 13th a few were seen in the water around the station. *Tima formosa* was not seen during the month, though in 1896 the species was abundant in Narragansett Bay.

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THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTHS OF JUNE, JULY AND AUGUST, 1898.

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THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTHS OF JUNE, JULY AND AUGUST.

During the month of June the temperature of the water continues the regular increase which begins on the first of April, and toward the end of the month reaches the temperature of 65° F. During July of the present year it fluctuated between 66° F. and 71° F., and during August it frequently registered 72° F.

With the increased temperature of the month of June there is a corresponding increase in the number of breeding animals; indeed, this month indicates the culminating point of reproductive activity of marine organisms at Woods Holl. The months of July and August are characterized by a constantly decreasing number of breeding animals, though the high temperature of the water is conducive to the rapid growth of innumerable larvæ.

Vertebrates.—Breeding lampreys have been taken at East Taunton as late as June 17, and the eggs hatch in from eleven to fourteen days. The smooth dog-fish, *Galeus canis*, frequently gives birth to ‘ pups ’ while confined in the ‘ fish cars ’ during this month. These young, beautifully marked, swim about with their parents, and do not seriously suffer from their restricted quarters. The fishermen say that the ‘ smooth dog ’ has two broods, and the observations made at the laboratories would indicate that this view is correct. The first brood is generally dropped during the early part of

June, though during the latter part of the month a few females are often found with fully developed young. It is probable that, as soon as the young are born, mature eggs leave the ovary and pass into the oviduct, where they become fertilized. Professor W. A. Locy has removed eggs from the oviduct, which were in segmentation stages, from as early as June 22 to as late as July 4. Through the early part of July the embryos are small, but during August only advanced stages are found. The second brood may be dropped as early as August 10th.

The belief that the females after giving birth to their first brood immediately breed again is supported by Dr. Ayers, who has noted that there are congested placental spots on the uterine walls of individuals, the oviducts of which contain active spermatozoa, and Dr. Locy has noted that the ovaries contain certain large ova during June, whereas they contain only smaller eggs after the early part of July. No individual, however, is actually known to have given birth to two broods in a single summer.

The sand shark, *Carcharias littoralis*, the most common shark at Woods Holl during the summer, so far as I know, has never been taken during the breeding season, all the individuals being apparently immature. The spiny dog-fish, *Squalus acanthias*, though at times abundant during the early spring, has not been taken in sufficient numbers during recent summers to be of special value. Those desirous of collecting embryological material of this species have generally gone to North Truro, Provincetown or Lanesville. During the latter part of June segmentation stages and early embryos are found. During July embryos of about 1 cm. prevail. Early in August the embryos have reached a length of about 2 cm., and during the latter part of August embryos from 3 to 7 cm. in length are most abundant.

The common skate, *Raja erinacea*, is abundant during June, July and August, and at times fully a bucketful of eggs have been deposited in the 'fish cars' in a single night. The ripe females may be distinguished by the color of the lower side of the abdomen, through the thin walls of which the ova may be felt and even seen. Torpedoes with ripe eggs have not been taken. The short-nosed sturgeon, *Acipenser brevirostis*, is occasionally taken in June, the females bearing ripe eggs. The menhaden, *Brevoortia tyrannus*, breeds during the month of June, though no young were taken the present year. By the middle of July schools of young fish of about one inch in length are often to be seen.

Fundulus majalis continues its breeding during June and early July, and its eggs may be artificially fertilized with the sperm of *Fundulus heteroclitus*. The latter species breeds abundantly from the middle of May until the middle of July, but during the latter part of July and the first of August only a few ripe eggs can be secured. *Cyprinodon variegatus* spawns in June. *Lucania parva* is said to be viviparous. I do not know when it breeds. I am informed that late in July the female pipe-fish bears large ovarian eggs, and the males are still carrying embryos in their brood-pouches. Late in August both embryos and pouches have disappeared, and the ovaries contain only immature eggs.

Two species of *Menidia* (*gracilis* and *notata*) abound in the neighborhood of the laboratories. The following has been taken from notes kindly furnished by Dr. C. Judson Herrick: On June 5, 1896, Mr. Edwards found *Menidia notata* spawning at Hyannis in vast numbers. At this time the fish had selected a point in the beach grass above the low-tide level, and at low-tide the eggs were consequently exposed to the sun and dried. Mr. Edwards noted great quantities of spawn and milt, and collected about a quart of the former. During the last days of June and the first ten days of July of the present year the fish were very scarce, though Dr. Herrick found a few ripe females and a very few males. The eggs adhere to each other in thick ropy masses, and to any foreign object with which they come in contact, by means of long threads. Both fertile and unfertile eggs sink to the bottom, and the first cleavage plane appears in about one hour. The eggs may be artificially hatched in jars of running water, the period of incubation being ten days. The young fish, which carry a small yolk-sac, are about 6 mm. in length. Fry were skimmed from the surface of the harbor on July 4th, and measured 1.5 cm. in length. On July 9th fry similarly taken measured 2.25 cm. in length.

The eggs of *M. gracilis* resemble those of *M. notata*, but the species seems to breed later, since many ripe females were taken during the first week in July. The eggs, however, do not undergo artificial fertilization as readily as those of the first species.

The mackerel, *Scomber scombrus*, breeds during the middle and latter part of June, and generally at some distance from the shore. During the early part of the month of August of the present year myriads of young fish, about two inches in length, were found in the southern portion of Massachusetts Bay, showing that the breeding had taken place much nearer the shore than is usual. The butter-fish, *Rhombus triacanthus*, breeds during June. The white perch, *Morone americana*, breeds in May and June, and the sea-bass, *Centropristes striatus*, from the middle of May to near the first of July. The scup, *Stenotomus chrysops*, spawns during early June, but the eggs do not all become ripe at the same time. Though thousands of squeteague were taken in the fish-trap during July, not a single individual contained spawn, and this was not surprising, for, according to Dr. Hugh M. Smith, spawning occurs about June. The cunner, *Tautogolabrus adspersus*, spawns during June and early July, and the bright colored young are abundantly found throughout the latter part of the summer. Ripe tautog, *Tautoga onitis*, were ‘ stripped ’ on June 15th, and ripe eggs might have been taken until the middle of July. The ‘ puffers ’ are also summer breeders, the spawning season occurring early in June, after which the young are frequently taken in the skimming-net.

Since the establishment of the biological laboratories at Woods Holl the toad-fish has contributed to science with great generosity. Tin cans, broken bottles and shattered fragments of crockery are regularly planted by the collectors, and are regularly lined with large golden eggs. Oviposition occurs as early as June 3, and it may occur at any subsequent time throughout the month. According to Dr. Hugh M. Smith the blue-fish arrives about June 1st, at which time well-developed ova are found in a small proportion, and at Nantucket large roes have been found as late as July 15th. The first young blue-fish were taken at Woods Holl on June 10th, and measured from 1¼ to 1½ inches in length. The young of the mullet, *Mugil curema,* 1¼ inches in length, were taken on June 28th. Both species of sea-robin breed during the early part of June. The eggs, not particularly transparent, readily develop in the laboratory and hatch in about five days. After the first of July females with eggs are seldom taken.

Among the Pleuronectidæ, *Bothus maculatus* breeds during early June, and the eggs may be artificially hatched, the period of incubation being about eight days. The young of 'flat-fish' were taken in the tow-net by Mr. S. R. Williams, from the 4th to the 17th of June, on which latter date they were most abundant. A few were also taken during the latter part of the month and during July. I have the following interesting note from Mr. Vinal Edwards: "A large school of young cod placed in the 'Eel Pond' directly from the hatching jars, in December last, left the pond in June when the water reached a temperature of about 60° F. They were at this time from 2 to 4½ inches in length." The spawn of the goose-fish is occasionally taken near Menimsha. When a spawn is found, an abundance of embryological material results since the eggs are united in a great jelly-like band that will more than fill a bucket.

The auftrieb is not rich in surface vertebrates during the summer. In June young hake, pipe-fish, lump-fish and herring occasionally occur. In early July young swell-fish, cunners, sticklebacks, tautog, sand-eels, silversides, hake and sand dabs ; and during the middle of July the swell-fish, cunners, sticklebacks, silversides, sand-eels and hake are still conspicuous, though gradually disappearing from the surface as the season advances. By the middle of August only occasional specimens are taken.

Two species of land turtles are abundant in fresh-water ponds near the laboratories. The painted turtle, *Chrysemys picta*, breeds from June 11 to 25, and deposits its eggs in the evening, from 6 to 8:30 o'clock. The snapping turtle also breeds during the middle of June, but it deposits its eggs in the early morning.

Ascidians.—I am indebted to Frank W. Bancroft for many of the following notes respecting the breeding of ascidians.

Appendicularia were abundant near Gay Head on July 28th, and *Doliolum* is often taken at the same locality. Farther from the shore several species of *Salpa* occur in abundance.

Among the simple ascidians, *Molgula* may be obtained in abundance from the woodwork in the harbor of New Bedford, and I think the eggs are ripe throughout the summer. *Cynthia partita* is apparently ripe throughout the month of July, at which time Dr. Bancroft also found ripe *Ciona intestinalis* and *Perophora viridis.*

Among the composite ascidians, *Botryllus gouldii* was found breeding from the sixth to the end of July, and almost all the older colonies contained either large ova or embryos. This species was not examined before the sixth, nor after the close of the month. Though several colonies of *Amarœcium stellatum* were examined, no large eggs or embryos were found during July, although *A. constellatum* frequently had large ova and embryos.

Crustacea.—There are several Brachyurans that carry eggs during the summer months. *Gelasimus minax, pugnax* and *pugilator* breed during the early parts of June, and females with eggs occur as late as July 2d, and perhaps later. *Sesarma reticulata* I frequently have found with eggs, but no specific data are at hand. *Pinnixa cylindrica* was found with eggs on July 13. *Pinnotheres maculatus* has been studied by Mr. F. P. Gorham, who found that the animals were very active at night, leaving the seclusion of the mantle-chamber of the mussel, and swimming and crawling about in the water in a most restless manner. On July 9 eggs in the earliest stages of development were taken, and from then until August 29 Mr. Gorham found all stages, though at the latter date egg-bearing females were relatively less abundant. *Panopœus* was found with eggs on June 7, and gastrulation stages were found on July 1. On July 8 all stages from four cells to complete embryos were noted, and on July 12 two females deposited eggs while in captivity. *Carcinus granulatus* was found with eggs, in late stages, June 25. *Platyonichus ocellatus* carried late stages on July 3. *Callinectes hastatus* was found with advanced embryos on August 3. *Libinia* has been seen to oviposit as late as August 7. *Pelia mutica* bears beautiful transparent eggs, which are in early embryonic stages the first week in July.

Among the Anomoura, *Hippa talpoida* carries eggs in the latter part of June and throughout the month of July. Mr. Gorham found early embryos and free-swimming young on August 9, 1896, and the characteristic Zoea are conspicuous in the skimmings throughout the month of August, being most abundant on the 22. Mr. M. T. Thompson found *Eupagurus longicarpus* with eggs until the middle of September. *E. annulipes* was not brought to the Laboratory before the early part of September, but at that time the females had eggs in varying stages of development. The breeding habits of *E. bernhardus* and of *E. pollicaris* were not noted, though the skimmings yielded an abundance of Zoea from the first of August throughout the month, and were probably present still earlier. The 'Glaucothoe stage' was first found on the 12th of August, and was frequent thereafter throughout the month.

Zoea of various species are conspicuous in the surface material from the first week in June, and Mr. S. R. Williams noted that when they were abundant they seemed to exclude 'Megalops' and *vice versa.*

Among the Macroura, *Gebia affinis* was found with advanced eggs on July 25. These hatched on August 7. *Callianassa stimpsoni* was found with eggs on July 1, and again on July 13. On the latter date the eggs were in segmentation stages. On July 18 other specimens bore advanced embryos which hatched on July 21. Dr. F. H. Herrick for several years had the opportunity of examining many lobsters at the Fish Commission Hatchery, and concluded that the larger number of eggs were laid during the latter half of July and the first two weeks of August. These eggs are normally carried by the female until the following spring, when they hatch during May, June and July. I regret that I have no specific data on the breeding habits of *Crangon vulgaris*, but I have every reason to suppose that it is bearing and hatching eggs with its characteristic industry. Mr. F. P. Gorham found *Virbius zostericola* carrying eggs in all stages of development from the first of June to the first of September ; the period of incubation lasts for about two weeks. *Palæmonetes vulgaris* was found with eggs in early stages of segmentation on June 20, and on the same date other individuals were found bearing late blastoderm stages and fully-formed embryos. The larvæ of *Palæmonetes* are excessively abundant in the auftrieb during July and August. The young of *Squilla* was occasionally taken in the townet during August, and was abundant on the surface of the Gulf Stream. A beautiful *Heteromysis*, bearing deep green eggs, was frequently dredged on the shelly bottom east of Nobsque during June and July. The young of *Cuma* were taken in the skimmings on June 14.

The Amphipods are by no means as abundant as during the spring. Mr. F. M. Watson found *Amphithoë compta* breeding through July and the first week or two of August and *Calliopius læviusculus* with eggs on August 1. *Orchestia agilis* was represented by innumerable young during the first two weeks in July; *Podocerus falcatus* was taken with eggs during the last two weeks of July and the first two weeks of August. Early in August a large number of Caprellæ bearing eggs were taken. *Talorchestia* has been found with eggs in late stages of development on June 14, and *Orchestia agilis* with eggs and embryos on June

20. A tube-dwelling amphipod, probably *Cerapus tubularis*, bears eggs, some of which are in early stages of development on July 4. *Hyperia* is frequently taken during June, and its large, almost absolutely transparent eggs would form excellent material for certain lines of biological research.

Among the Isopods, *Idotea robusta* was found with eggs on July 17, and again on August 12. Dr. J. P. McMurrich has found *Jæra marina* breeding in the middle of June, when his first observations were made, and from then without interruption until the first week in September, the time of his departure from the laboratory. *Tanais vittatus* was found with eggs in various stages of development early in August, and Dr. W. M. Wheeler has found the eggs of *Armadilidium vulgare* around old logs at Butler's Point late in June.

Copepods are, of course, abundant in all the surface material, and the parasitic Copepods found attached to the various fishes almost invariably bear egg-capsules which contain embryos in various stages of development. Attached to the floating seaweeds, boards, etc., which are washed on to the shore from the ocean are two or three species of 'goose barnacle,' which yield abundant embryonic material.

Dr. Wheeler found *Limnetis gouldii* breeding in small fresh-water onds on Penzance, June 6–13, 1892. Associated with these were many specimens of *Eulimnadia agassizii* and *Bosmina*, both sexually mature.

The Pycnogonids breed during July, August and September. Dr. T. H. Morgan has recorded the appearance of *Tanystylum orbiculare* with eggs on July 1st; *Pallene empusa* carries eggs throughout the summer, and *Phoxichilidium maxillare* during August and September.

Limulus was found depositing eggs on June 19, and eggs were artificially fertilized on July 12, though the females were then nearly spent.

Vermes.—The breeding season of *Lepidonotus* and *Harmothoë* has passed. The eggs of *Sthenelais* may be artificially fertilized, and ripe individuals have been taken during the middle and latter part of August. *Podarke obscura* begins to oviposit about July 1. Dr. A. L. Treadwell has succeeded in artificially fertilizing the eggs by keeping the males and females in separate dishes until the sexual products are extruded, and then mixing in the ordinary way. *Autolytus* and other Syllids are frequently taken in the skimmings; the eggs are held in small spheres under the abdomen. *Nereis limbata* and *N. megalops* may be taken at the surface, in the evening, in great numbers and during the entire summer. The breeding habits of *Diopatra* are unknown, though the ova are nearly ripe in August. Though many specimens of *Marphysa* have been collected, the time of sexual maturity is not known. The breeding habits of *Anthostoma* and *Trophonia* are also unknown. Dr. A. D. Mead informs me that *Cirratulus grandis* breeds during July, and that the females will deposit their eggs while in confinement. The eggs are of fair size, but very opaque. Oviposition takes place in the evening. On the breeding habits of *Maldane* and *Cistenides* I have been unable to collect specific data.

Dr. Mead has spent a great deal of time in determining the breeding period of *Amphitrite ornata*, and after collecting about eight hundred specimens, at various times of the year, concludes that there is no definite breeding season. Between the first of June and the last of August only occasional individuals were found which yielded ripe sexual products. The eggs are extruded during the evening, and will not fertilize if artificially removed from the body cavity. *Scionopsis palmata* was found to bear eggs, apparently ripe, in August, but artificial fertilization was not attempted. The eggs of *Serpula* (*Hydroides*) may be readily secured by simply crushing the worm-tubes, and then placing the somewhat injured female in sea-water. As soon as the males are taken from the tubes the sperm will be seen to ooze from the nephridial openings. *Spirorbis borealis* is frequently found with eggs and embryos. From the latter part of June to the latter part of July the eggs of *Arenicola* may be collected by the bucketful. They are extruded in a jelly-like mass, sometimes two feet in length, and are especially abundant on the warm sand-flats of Buzzard's Bay.

Dr. Mead obtained the eggs of *Chœtopterus* during July and August by cutting open the females. During the early summer of 1892 the larvæ of *Polygordius* were exceedingly abundant, and few specimens were taken during the past summer. *Sagitta* occurred occasionally. It was noted by Mr. S. R. Williams during the middle of June, and again at the close of the month and early in July.

Nectonema was occasionally brought into the Laboratory, and Dr. H. B. Ward has known it to extrude its eggs while in dishes of sea-water.

Dr. E. G. Gardiner informs me that he

has taken the orange-colored eggs of *Polychœrus caudatus* as early as June 6, and that they are abundant from June 15 to August 25. The eggs are deposited at night in transparent gelatinous capsules.

'Tornaria' larvæ are often taken during August in great abundance at flood tide, during both day and night.

Echinoderms.—Previous notes in SCIENCE have called attention to the early breeding habits of several representatives of this group. *Echinarachnius parma* continues to breed throughout June and the early part of July, and a limited number of eggs may be secured even during the later portions of the summer. *Arbacia punctulata* yields ripe eggs during the latter part of June, throughout July and a portion of August. *Strongylocentrotus* was not carefully examined, though at Nahant I have often noted the extrusion of the yellowish, opaque eggs at various times during the warmer months.

The breeding habits of the star-fish are peculiar. Dr. A. D. Mead has found the breeding period to culminate in Narragansett Bay during the last week of June, although at Woods Holl no considerable number reached sexual maturity at any time during the past summer. In 1892 larvæ were abundant on June 18.

Mr. Caswell Grave paid particular attention to the Ophiurids during the past summer, and was successful in getting many ripe specimens of *Ophiopholis aculeata* at Nahant during the month of June. These he brought to the Laboratory in sea-water, artificially cooled, and they deposited their eggs and sperm between eight and nine o'clock in the evening of the day they were collected. The development was slow, the 'pluteus stage' being reached not until three weeks after fertilization, and several of the plutei lived to be thirty-three days old without showing signs of metamorphosis. Mr. Grave followed the development of the sexual glands of *Ophiura olivacea* with great care from the first of June, but the period of sexual maturity was not reached until the second week of July, when a limited quantity of fertilized ova was obtained. The larvæ proved to be quite different from those of any previously described Ophiuran. *Thyone briareus* and *Synapta inhærens* (= *Synapta girardii*) probably breed during June and July. I think the eggs have never been artificially fertilized. Echinoderm larvæ, which may have been brought to Woods Holl by currents, were abundant during the middle of June. Brachiolaria swarmed in Narragansett Bay from the last of June to the middle of July.

Mollusks.—During the first week of June the young of *Mytilus*, the 'sand-collars' of *Lunatia*, the 'eggs strings' of *Sycotypus* and the 'egg-capsules' of *Urosalpinx* were noted in Narragansett Bay. During the second week of June, *Crepidula*, *Urosalpinx* and several naked Mollusks were found ovipositing. Dr. F. R. Lillie has collected eggs of *Pecten* from July 10 to August 4. On August 17 the breeding period had passed. According to Dr. Conklin the breeding period of *Crepidula fornicata* lasts from early summer until about August 15. The breeding period of *Crepidula plana* is somewhat later and longer, and newly laid eggs were found September 7. *Crepidula convexa* lasts through much the same period as *C. plana*. Dr. Lillie says that the unsegmented ova of *Unio complanata* can be obtained from about the middle of June to the middle of July, those of *Anodonta* toward the end of July and early in August. The 'Glochidia' of *Unio* escape in August and September, and the eggs of *Anodonta* are carried by the mother through the winter and are extruded in the spring.

Small squid were taken on the surface from June 20 to the close of the summer.

The clam, *Mya arenaria*, breeds during June and perhaps earlier. The height of the breeding season of the oyster is during the latter part of July, and the development is so rapid that the young swim in less than six hours after fertilization.

Mr. S. R. Williams, who kept a record of the surface forms during the past summer, found 'veligers' abundant on June 12, July 9 and July 19.

Cœlenterates.—*Cyanea arctica* has been taken with ripe eggs as late as June 3, though by the middle of the month only occasional specimens are seen. The eggs readily fertilize, and the young develop freely in the aquaria. The 'Ephyræ' of *Aurelia* were taken in the tow on June 15. The Scyphomedusæ are not abundant at Woods Holl during mid-summer, an occasional *Dactylometra* or an immature *Cyanea* being almost the sole representative of the group. At New Bedford, and in Narragansett Bay, *Dactylometra* is excessively abundant, and one would probably have little difficulty in getting material for embryological study at almost any time. *Metridium* has frequently been seen to extrude its eggs, which may be artificially fertilized, and *Sagartia* has also been found breeding during the middle of July.

I am indebted to Professor W. C. Hargitt for many of the following notes on the breeding of Hydroids:

Clava leptostyla.—Colonies are occasionally taken from rock-weed in the 'Hole,' from June 18 to the end of the month, and less frequently throughout the summer. Colonies may also be taken from exposed timbers under the wharf of the U. S. Fish Commission. The male colonies are much more abundant and conspicuous.

Clytia bicophora, on the shells of *Mytilus*, with colonies of *Eudendrium*, is abundant late in June, when it is in a thrifty condition, and with mature gonangia.

Eudendrium. — Colonies of *Eudendrium*, probably *E. ramosum*, were taken in very imperfect condition June 17, apparently just beginning development from old stolons. Specimens were also taken from under the culvert at the outlet of the Eel Pond, on June 20, in a more vigorous condition, but with only male gonophores, which contained ripe spermatozoa. Colonies developed rapidly during the following ten days and produced female gonophores. The earliest signs of development of eggs occurred during the first week of July. The latest were recorded by Dr. Murbach, on September 15.

Corynitis Agassizii.—Specimens taken from the wharves of the Fish Commission on June 20, on shells of *Mytilus*, were in a thrifty condition and bore mature medusæ. These are set free during the early evening, and swim actively about the aquarium, though at this time there are no indications of sexual products. Several colonies of this interesting Hydroid were taken, but always from the encrusting deposit of a Bryozoon, which frequently occurs on the shells of *Mytilus*.

Hydractinia (*Echinata*) *polyclina.*—Colonies taken from the shells of Eupagurids, from rock-weed and from *Limulus*, were mostly sterile in June, or with only male gonads. It breeds during July and August.

Margelis carolinensis is quite common and in an excellent state of growth during June, though without medusa-buds. It is found on the timbers of the Fish Commission docks, on rock-weed and occasionally upon eel-grass. It breeds during August.

Obelia sp.—A species of *Obelia* is very abundant along the rock work and wharves, and during June develops apparently ripe gonangia, though few free medusæ.

Parypha crocea.—In splendid profusion and perfection throughout the month of June.

Pennaria tiarella.—During the month of June this species is to be found in limited numbers attached to rock-weed and to the piles of the wharves. Its development is slow, specimens with medusa-buds not being taken until June 29. During the following weeks the development is more rapid, both of the polyp-stock and of the medusæ. Dr. Murbach has found the species breeding as late as September.

Sertularia sp.—Everywhere in abundance, but with gonangia only in a few cases. Several species are found, of which the commoner are *Pumila* and *Argentea*.

Dr. McMurrich found *Laomedea amphora*, on Fucus, with ripe gonophores, June 2, and associated with it was *Halecium*, in a similar sexual condition. During the latter part of June and throughout the summer the medusæ of *Gonionemus* is found in great quantities in the Eel Pond. Mr.

Williams noted *Clytia* and *Lizzia* in the surface fauna during the second week of June, and medusæ of *Eucope* were found at various times during the summer. On July 28 an undetermined species of Hydromedusa was so abundant at Menimsha that a tumbler simply dipped into the ocean would be more than half filled with them.

Dr. Murbach has found *Corynitis* breeding during July and the early part of August, *Podocoryne* and *Hypolytus* during August.

Ctenophores, frequent during the early part of summer, literally swarm during the latter part of August. *Mneniopsis* is the most abundant species.

H. C. Bumpus.

THE BREEDING OF ANIMALS AT WOODS HOLL DURING THE MONTH OF SEPTEMBER, 1898.

By M. T. THOMPSON.

Science, N. S., Vol. IX, No. 225, April 14, 1899.

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THE BREEDING OF ANIMALS AT WOODS HOLE DURING THE MONTH OF SEPTEMBER, 1898.

WITH the month of September the record of the breeding habits of the summer fauna practically closes. Very few of the species continue to breed into October. The auftrieb, though less rich in species, is at the beginning of the month similar to that of late August, but after the first week the number of forms steadily decreases. It consists for the most part of crustacean larvæ, the bulk of the material being brachyuran and eupagurid.

The temperature of the water was constant at 72° F. for the first week. It then fell steadily until the 25th, when it reached 65° F., and remained at this point until the close of the month. The density varied from 1.0208 to 1.0225.

Vertebrata. The fishes present no features of special interest, as the summer forms are still present, and no species is breeding. The surface skimmings show a few fry at intervals. On the 20th one or two larval flatfish, in which the eyes had just begun to migrate, were taken. About the 25th three smooth dogfish, *Galeus canis*, which had been confined in the ‘Pool,’ were killed, and twenty-seven embryos, 10 to 11 cm. long, were found in the oviducts.

Crustacea. None of the adult brachyura examined were breeding. Zoëæ were conspicuous in the auftrieb during the early part of the month, and later various megalops were abundant.

The zoëa of *Callinectes hastatus* was the most abundant form, lasting about two weeks. The megalops of this species was plentiful at all times, particularly on the 18th. Specimens in the laboratory changed to the beautifully-spotted 'first adult' on September 27th, 29th, and October 3d. Another zoëa (which I have not identified) was very abundant in the latter part of August and the first week of September, disappearing about the 11th. It resembles the zoëa of *Callinectes*, but has a longer rostrum and dorsal spine, and the exopodite of the antenna is a straight blade as long as the rostrum.

Among the Anomura, the larvæ of *Hippa* had disappeared on September 4th. Eupagurid zoëæ swarmed in August and the first week in September, and were present in decreasing numbers throughout the month. The 'glaucothoë-stage' was abundant at all times. Data relating to the breeding of *Eupagurus bernhardus* and *E. pollicaris* are scanty, but the few females of the latter species which were examined were without eggs. *E. annulipes* was brought in on the 4th, when a few were bearing eggs in early stages of development. Females of *E. longicarpus* with eggs were taken as late as the 13th.

Among the Macroura, specimens of *Virbius zostericola* had eggs in the later stages on the 11th. Larvæ and young adults, ranging in length from 5 mm. to 10 or 15 mm., were present in the skimmings. Those of small size persisted throughout the month. *Palæmonetes vulgaris* was not breeding, but the larvæ (mostly the 'fifth' and 'sixth' stages of Faxon) were occasionally taken, and toward the end of the month several of the 'first adult stage' were found. A specimen of *Crangon vulgaris* with eggs was obtained on the 19th. *Heteromysis*, dredged at Vineyard Haven on the 12th, and off Nobska Point about a week later, had well-advanced eggs in the brood-pouch.

No adult Isopoda were examined, but immature *Idotea robusta* and *I. irrorata*, ranging in length from 2 mm. upward, frequently appeared in the skimmings.

Among the Amphipoda, a minute form, apparently a species of *Montagua*, was very common among the hydroids. On September 21st nearly all were carrying eggs in various stages of development. Many *Caprellæ* obtained at the same time bore embryos approaching maturity.

Squilla larvæ (5 mm. long) appeared at intervals throughout the month. Copepods were abundant at all times. *Diastylis* was taken in the evening and is apparently attracted by any artificial light. On the 12th a number of 'Goose Barnacles' had eggs in all the later embryonic stages, and some began to liberate nauplii about this date.

Mollusca. *Scycotypus* continued to deposit its 'egg-strings' during the first two weeks of the month. The breeding period of *Crepidula fornicata* had closed, but on the 19th I found a few specimens of *Crepidula plana* with eggs in early cleavage stages. The breeding period of *Littorina littorea* in American waters is not known. On the 20th great numbers of young, about one millimeter in diameter, were found on the rocks at Nobska Point. During the latter part of August and the early part of September, Veligers, all apparently of one species, were conspicuous in the surface skimmings; these disappeared at about the time that the young *Littorina* were found.

Vermes. Mr. R. H. Johnson found *Bugula turrita* liberating embryos, even after the middle of the month.

Small specimens of *Nereis limbata* and certain allied forms occurred sparingly in the auftrieb. On the evening of the 30th *Autolytus* was still fairly abundant, and many of the females were carrying eggs in early stages of development. *Rhyncobolus* and *Diopatra* were not breeding.

Cœlenterata. With the exception of one or two minute forms, no Medusæ were found. *Gonionemus* was abundant in the Eel Pond, and specimens brought into the laboratory about the middle of the month extruded eggs. The greater part of these eggs did not reach the blastula, and none developed beyond this stage. Ctenophores *Mnemiopsis*, very conspicuous in late August, appeared in increasing numbers during September. *Obelia*, with a few ripe gonangia, was obtained on the 21st. *Pennaria tiarella* formed the bulk of the abundant hydroid-growths on the Fish Commission wharves, although a *Erudendium*, probably *E. ramosum*, was plentiful. Here and there small patches of *Plumularia tenella* were found. East Chop and Edgartown were visited on the 12th. At the former place there were few colonies of *Pennaria*, but a great abundance of *Eudendrium* and *Plumularia*. At Edgartown I did not find either *Pennaria* or *Eudendrium*, but *Plumularia* occurred in dense masses, which literally covered the submerged woodwork of the wharves.

At Woods Hole the colonies of *Plumularia* were small and sterile, while at the other localities they were large and provided with gonangia in the various stages of development.

The *Eudendrium* and *Pennaria* bore medusa-buds in all stages, and the latter species remained in fruit as late as the 21st, and perhaps later. M. T. Thompson.

PERIDINIUM AND THE "RED WATER" IN NARRAGANSETT BAY.

By A. D. MEAD.

Science, N. S., Vol. VIII, No. 203, November 17, 1898.

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PERIDINIUM AND THE 'RED WATER' IN NARRAGANSETT BAY.

During the last two months the inhabitants of Rhode Island witnessed the following remarkable phenomenon. The water of a considerable portion of the Bay became thick and red, emitting an odor almost intolerable to those living near by. The situation became alarming when, on the 9th and 10th of September, thousands of dead fish, crabs and shrimps were found strewn along the shores or even piled up in windrows.

At the request of the Rhode Island Commission of Island Fisheries, an investigation was made to determine the cause and extent of the unusual color of the water and of the great mortality of the fish. The results of this investigation are briefly as follows

During the last of August, throughout September and a part of October streaks of red or 'chocolate' water were observed from near Quonset Point and Prudence Island, north to Providence, and, on the flood tide, up the Seekonk River, nearly to Pawtucket, a range of about fifteen miles. In other parts of the Bay, as far as could be learned, the phenomenon had not been observed.

On the 8th and 9th of September the water became extremely red and thick in various localities from East Greenwich to Providence, and the peculiar behavior of the marine animals attracted much attention. Myriads of shrimps and blue crabs, and vast numbers of eels, menhaden, tautog and flatfish came up to the surface and to the edge of the shore as though struggling to get out of the noxious water. Indeed, the shrimp and crabs were observed actually to climb out of the water upon stakes and buoys and even upon the iron cylinders which support one of the bridges and which must have been very hot in the bright sun. In several instances, on these two days, hundreds of blue-crabs were caught by a single individual in a few minutes' time, at the mouth of the Seekonk.

On the following day, September 10th, and for several days afterwards, hardly a live crab or shrimp could be found. Along the shores, however, in the same vicinity, cartloads of dead shrimp were piled up in windrows, and among them were strewn great numbers of crabs and fish of various kinds, especially menhaden and eels. This singular behavior and alarming mortality of marine animals was reported from nearly every station at which the red water occurred, and from no other station, which indicates that the two phenomena are related as cause and effect.

It was commonly believed that dye-stuffs or other refuse emptied into the rivers at the upper part of the Bay gave to the water its color and unpleasant odor, but microscopic examination showed that the water was swarming with minute organisms, species of *Peridinium.* The *Peridinium* is reddish brown in color and occurred in such excessive abundance that it gave to the water its peculiar color and odor, besides making it so opaque that one could hardly see a white shell six inches below the surface.

With regard to the systematic position of this organism there is a difference of opinion. It is, in fact, ranked with the animals by some authors and with the plants by others. I have not yet been able to determine the species of our *Peridinium.* It resembles in many respects Carter's *Peridinium sanguineum ;* it is much flattened, and the anterior end is distinctly bilobed, like *Peridinium tabulatum,* though the lobes are more rounded. Besides a flagellum extending forward from the ventral groove, a very large flagellum lies in the equatorial sulcus and entirely encircles the body. No cilia could be demonstrated.

After September 9th and 10th, when the great mortality of fish occurred, the *Peridinium* became, for a few days, less abundant, and then increased again until the 23d. There was a heavy rain on the 23d, and on the following day the water was comparatively clear. Since this date it has been more or less in evidence up to the day of writing (October 7th). On September 21st the number of *Peridinium* per cubic centimeter in the Seekonk River was estimated at 5,880. This was enough to give the water a very noticeable red color. Nevertheless, the marine animals appear not to have been seriously affected since September 10th or 11th, though the approach of a streak of red water has, in some instances, interrupted good fishing.

In the Seekonk River the shrimp and crabs gradually returned, and in about three weeks after the sudden mortality were nearly as numerous as before, though the water was at times distinctly colored. On the 23d some shrimp, oysters and small fish (*Fundulus*) were kept in the water where the *Peridinium* were the thickest, and suffered no apparent injury. In consideration of these facts, it has been doubted whether the *Peridinium* was the immediate cause of the peculiar behavior and death of the fish which occurred on the 9th and 10th of September, especially as the weather had been phenomenally hot for several weeks previous to that date. I believe, however, that the *Peridinium* was the cause of the trouble, and not the hot weather nor manufacturers' waste, for the following reasons:

On the two or three days in which the mortality took place the water was extremely red.

The hot weather was followed by a cold wave a day or two before the mortality commenced.

The phenomena occurred in Greenwich Bay and off Nayatt, many miles from any considerable source of contamination.

Finally, the phenomena in question were noticed by very many persons throughout the whole range of the red water, while in neighboring portions of the Bay, for example, in the Warren River and in Bristol Harbor, where the temperature of the water is quite as high as in the red-water districts, no *Peridinium* and no mortality or unusual behavior of the marine animals was reported, though the regions were carefully canvassed.

There are many recorded instances of salt and of fresh water colored red probably by *Peridinium* of this or a similar species. H. J. Carter, in his account of 'The Red Coloring Matter of the Sea round the Shores of the Island of Bombay,' described the new species *P. sanguineum*, which produces this effect. He points out, also, that Darwin's description of the animalcule which he found to color the sea red, a degree south of Valparaiso, accords exactly with that of *Peridinium*. The animalcules which, according to Salt, produce the red color in the Red Sea, may also be due to this form, and the same cause may perhaps be ascribed to the red color of the sea off Iceland in 1649. Porter quotes "the following passage from an eye witness of a similar occurrence at Porebunder, on the coast of Khattywar, India, where the red water is extremely common, viz.: 'the color of the sea water on Saturday evening last, the 27th of October, 1849, was changed from its usual tint to a deep red, emitting a most foul smell; the fish speedily were all destroyed and washed upon the beach in large quantities, etc.'" Though the narrator believed that this might be due to a submarine eruption of mud, Mr. Carter is inclined to ascribe it to some 'animalcule,' most probably *Peridinium*. He also directs attention to the Mosaic account of the plague of Egypt given in the following verses: "And all the waters that *were* in the river were turned to blood." "And the fish that *was* in the river died; and the river stank, and the Egyptians could not drink of the water of the river; and there was blood throughout all the land of Egypt."

A. D. MEAD.

OBSERVATIONS ON THE SOFT-SHELL CLAM.

By A. D. MEAD.

Thirteenth Annual Report of the Commissioners of Inland Fisheries
of Rhode Island, made to the General Assembly at its January Session, 1900.

OBSERVATIONS

ON THE

SOFT-SHELL CLAM.

By A. D. MEAD,
BROWN UNIVERSITY.

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of Inland Fisheries, made to the General Assembly
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OBSERVATIONS ON THE SOFT-SHELL CLAM.

BY A. D. MEAD, BROWN UNIVERSITY.

The following "comparative statement of the yield of clams in the New England States during a series of years" shows of what importance the clam industry has been in our State. It shows also a very considerable decrease in the yield of clams since 1880, and at the same time a marked increase in the price per bushel.

The statistics were arranged by Dr. Hugh M. Smith, of the U. S. Fish Commission, and with the exception of one item, were published in the report of the Commissioner for 1894. Through the kindness of Dr. Smith the data for Rhode Island for 1898 are added.

Maine.

	Bushels.	Value.
1880	318,383	$101,808
1887	608,780	228,490
1888	600,675	227,665
1889	595,105	200,761
1892	416,806	157,431

New Hampshire.

1880	17,960	$8,980
1887	280	140
1888	300	150
1889	300	150
1892	1,050	975

Massachusetts.

	Bushels.	Value.
1880	158,626	$76,195
1887	230,659	121,202
1888	243,777	127,838
1889	240,831	137,711
1892	191,923	133,529

Rhode Island.

1880	53,960	$48,564
1887	25,825	25,030
1888	30,825	30,030
1889	33,375	32,475
1892	33,950	45,222
1898	15,015	20,569

Connecticut.

1880	75,000	$38,000
1887	26,735	25,370
1888	26,575	24,270
1889	26,360	24,900
1892	23,780	25,320

Total.

1880	623,929	$273,547
1887	892,279	400,252
1888	902,152	409,953
1889	895,961	395,997
1892	667,509	362,477

The Extent of Shore in Narragansett Bay Available for Rearing Clams.

From its geographical peculiarities, our State is particularly well adapted for clam culture; the Bay has a long shore line for so small a body of water, on account of the many peninsulas, estuaries, and islands, and nearly all the shore is protected from the heavy seas. In order to ascertain how much of the shore in this State is suitable for the growth of clams, a preliminary survey of the bay was made.

Through the courtesy of the United States Fish Commission, the steam launch Blue Wing was detailed to aid in collecting this information, together with data concerning the location of fish-traps, and the density and temperature of the water in various parts of the Bay. A considerable extent of the shore was examined directly, but for most of the information we are indebted to numerous fishermen and other residents, who from long experience have particular knowledge of certain localities.

There are in the aggregate more than fifty miles of shore which is considered good clam ground, and this is not limited to any portion of the Bay, but is found in all parts, wherever in fact there is soil enough for the clams to bury themselves. It is not by any means necessary that the ground should be soft, for hard clay and exceedingly stony ground often yield a good crop of clams. In many localities, also, no clams occur above the mean low-water mark, while they are comparatively abundant lower down and can be dug in the ordinary manner when the tide is uncommonly low. Nowhere, however, are the clams abundant to-day, and it is the common testimony from all parts of the Bay that, although they were exceedingly abundant from ten to twenty-five years ago, they are now comparatively scarce. The shores are, at present, almost depleted, and the difficult process of "churning" them in several feet of water is often resorted to by those who make a business of supplying clams to the market.

The set of clams was exceptionally large last summer (1899) in various parts of the Bay, for example about Green's Island (Conimicut), at Wickford, in the Kickemuit river, and on Oakland Beach. It will be interesting to observe how long the clams will remain abundant in these localities.

Since the above was written, on February 5 and 6, (1900), there were a great many bushels of extremely large clams in the markets.

They were taken from the flats in various parts of the bay at Wickford, the Kickemuit river, and other localities, when the tide was phenomenally low. One of the largest specimens, taken from Wickford, measured 5¾ inches in length and weighed 15 ounces; and a bushel taken at random from the market contained only 119 clams.

Egg-Laying, and Habits of the Very Young Clams.

The eggs of the clam, like those of the oyster, are exceedingly minute. Like the latter, also, they are extruded into the water where they are fertilized, and where they develop into free-swimming larvæ. The exact limits of the egg-laying period of the clam have not been determined, but it probably extends through the months of May and June, as Dr. Kellogg conjectured in the last Report.

On the eighth and on the twelfth of May the clams examined at the Kickemuit river were full of sexual products, which appeared under the microscope to be nearly ripe. On May 22 I succeeded in fertilizing some of the eggs artificially by dissecting them out into a dish of sea-water and adding the sperm taken from the male clam in the same way. The early stages of development were regular and apparently normal, but, unfortunately, I could not remain at the house-boat to care for the eggs, and they died. The experiment proved, at least, that the clams were ready to breed toward the last of May, and that it is possible to fertilize the eggs artificially.

On May 29 a silk net was obtained which was fine-meshed enough to hold many of the free-swimming young of the clam, and from this date until the second week of July these minute clams were taken at Wickford almost every day by dragging the net along the surface of the water.

The specimens caught in this way are hardly visible to the unaided eye. By the aid of the microscope they are seen to have two shells hinged together, and in this respect they resemble the adult clam. In order to procure them for examination the skimming-net is shaken out in a dish of water. The clams may then be separated from the myriads of other small organisms by gently tapping the dish, when they will stop swimming, close their shells, and fall to the bottom. They are then easily picked up with a pipette, and transferred in a drop of water to a watch crystal under the microscope. When first caught they vary considerably in size, some being four times the diameter of others, as shown in the figure (Fig. 1). As one watches these specimens under the microscope he will frequently see one of them open its shell, thrust out and expand a circular swimming-organ and go whirling about in the water for a while; then as suddenly, this organ, the velum, is drawn in, the shells close over it, and the clam falls to the bottom and remains quiet. Figure 4 is a free-hand sketch of one of these swimming clams (caught on May 29) with the swimming-organ expanded. Around the margin of the latter are the rapidly moving cilia, which create a current of water in the direction indicated by the arrows. This specimen had struck a snag, and was held by it while the sketch was made; smaller organisms and particles of dirt were swiftly swept backwards, meanwhile, by the energetic strokes of the cilia. In the midst of the organ is a long, slowly moving flagellum or lash, which may, perhaps, serve as a feeler.

Inasmuch as there are no published figures of the clam at this stage, it was not possible upon the mere examination of these creatures to say definitely that they were the young of the soft-shelled clam. It was presumed that they were, however, not only from their appearance but from the fact that the adult clams a week or two before were ready to lay, and, further, from the fact that by the last of June the young set of clams is well started. (See Kellogg's Report, 1898.) The absolute proof that they were clams was forthcoming, however, for a number of specimens were isolated and kept alive in dishes for several weeks. During the first week or two they grew considerably, lost their swimming-organ, and took on unmistakable characters of the soft-shelled clam. Figure 2 is from a camera drawing of one of these living clams two weeks after it was caught, *i. e.*, on June 14. It is drawn to the same scale of magnification as those in figure 1. The shape of the shell has been greatly changed, and the clam is more than twice the length, and many times the bulk, of even the largest specimen when first caught. The siphon (snout), gills, liver, stomach, and heart, and the relatively large foot have been developed, the internal organs showing plainly through the transparent shell. Figure 3 represents the same individual, drawn with the camera, to the same scale, ten days later, on June 24. The body is now still further elongated, the gill-plates are considerably more numerous, the foot is, perhaps, somewhat larger in proportion, and a peculiar sense organ, the so-called ear, is plainly visible within the substance of the foot. The lines of growth, which can be easily made out upon the shells themselves, show the changes in shape which have taken place during the process of growth. Although the rate of growth in this specimen is seen to have been quite rapid—from the size of one of those in Fig. 1 to that in Fig. 3 in less than three weeks—it was doubtless much less rapid than it would have been under natural conditions; for this specimen was kept in a dish, the water being changed only a few times, so that the supply of food, which consists of microscopic organisms, was very meagre as compared with that in the tide-water.

Among the clams caught in the skim-net there were usually many in which the foot and siphons were already developed. Such specimens, when watched under the microscope, would crawl about by means of the foot instead of swimming; yet they must have been able to swim, since they were taken near the surface of the water. I am not certain whether the swimming-organ was still capable of being used, or whether they swim with the foot. The latter method I would have thought almost impossible had I not seen it in use by razor clams which were many times larger. On the evening of July 20 a large number of razor clams, some of the latter measuring seven millimetres (more than a quarter of an inch), were taken in the tow-net. The shells were well-formed and hard, but the animal swam rapidly about by means of a curious kicking stroke of the very long foot. They were never taken in the tow except on this occasion, a rainy evening when a strong wind was blowing.

Whatever method of swimming the young clams may finally use, it is certain that they swim freely in the water until the foot and siphon are developed and they are thus equipped for crawling about over the sea-weed, stones, sand, and other objects they happen to strike upon.

A specimen whose swimming-days were past is represented in Fig. 5. The double nature of the siphon is shown at this stage, the incurrent and excurrent portions being almost separate from each other. The dotted lines represent the foot as it appears when the shell is closed, and the foot thrust out is represented by the solid lines. It is impossible to obtain more than a hasty camera sketch of the outstretched foot because its movement is so quick. The foot reaches out sometimes considerably further than the picture indicates, takes hold of the bottom of the dish, and with a quick jerk the shell is pulled up to it, the whole operation not occupying more than a second or two. By this rather clumsy method of travelling the clam is able to make considerable progress.

A few days after the clams are caught at the surface they are found to have attached themselves to the bottom of the dish or to any object which happens to be near them. Kellogg found last year these very small specimens attached to sea-weeds and other objects and carefully studied their habits from this period of life, when they are less than one-fiftieth of an inch in length, until they are finally settled in the ground. He showed that they attach themselves to objects by spinning byssus threads as the mussels do, but that they can at pleasure release themselves from the attachments, crawl about and attach themselves again. The ability to attach itself remains until the clam is upwards of one-half an inch in length, and by this time most of the clams which survive have buried themselves in the ground. Fig. 24 is a life-size photograph of a small clump of clams anchored by byssus threads to a mussel-shell and to stones. As Kellegg pointed out, this capacity is of greatest advantage to the clams; for those which happen to set upon sea-weed, stakes, stones, etc., are able, with some degree of safety, to wander about until they find a suitable place in which to burrow, and those which are not satisfied with the ground where they first burrow can come out and go to a new place, as they were actually seen to do. Of the greatest utility, however, is the habit of anchoring themselves in the burrow so that they cannot be so easily washed out.

While the rock-weed and other algæ are of great service to the clams in furnishing them with a convenient temporary lodgment where they will not be smothered by the silt when they are very small, it is true also the clams set in great quantities and grow in some sandy beaches where there is no sea-weed.

Some General Features of the Clam Set.

By the first week in July, 1899, a great many clams had already found their way into the sand. At this time they were so small that they escaped general notice, ranging from a size at which they were hardly visible to 9 millimetres in length. (See Fig. 6). By the third week in July a great majority had burrowed, and then there were probably more of this year's clams in the sand than at any other time during the year, for during the next few months they were destroyed in enormous quantities. Although the free-swimming young were, in their season, abundant at all times and at places in the water of the harbor (Wickford), the set of clams which was found buried in the sand was very unevenly distributed. The sandy shore in some places was literally filled with them from below low-water mark to about the half-tide mark. Here it would be impossible to pick up a handful of sand without taking up with it several clams. Within a few rods of these specially fertile areas however, in the same sort of soil, only a comparatively few clams were to be found—not one-thousandth as many as in the former places.

It was very apparent in these cases that the abundance or scarcity of the set was not due to the quality of the soil nor to the quantity of old clams in the vicinity, nor yet to the absence of enemies, but was due probably to the position of the shore with reference to the tide currents. Some of the areas where the set was exceedingly thick were, moreover, far from being the best for adult clams, and the reason is not far to seek. In one case a certain point of shore was set in the middle of July as thickly as the clams could burrow, but by the ninth of August hardly a young clam could be found. They were apparently washed out or were covered with shifting sand. In another locality, about 40 rods from the last, the set was discovered on July 5 and was also very thick. These clams continued to be abundant throughout the summer and autumn, and, though meanwhile they were somewhat thinned out, were yet very numerous on December 4. The thinning out began in July, and from this time until September there was always a wind-row two or three feet wide of small clam-shells along this portion of the shore. Very often among these shells one would find live clams and preying upon them a whole army of star-fishes, crabs of various species, and mummichogs. Undoubtedly the crabs, especially the blue crabs "paddlers," and some other animals dig up or uncover the young clams and scatter them about where they fall prey to many enemies; but I think one important factor in their wholesale destruction lies in the fact that they set much thicker than they can grow and a great many are crowded out, or, at least, if they are once brought to the surface of the ground, cannot burrow again. When the clams are not more than one-fourth of an inch long—early in July—they were near together, but when by the last of July they had become several times longer and many times the bulk, they actually touched each other; for at this period they all buried themselves to about the same depth. As one walked over the ground, or tapped it, the whole surface for a yard or two would move perceptibly as the clams contracted.

A more definite notion of the abundance of the clams in the locality mentioned above will be gained from the following: On August 9, after they had become somewhat thinned, a square yard on the shore was staked out and the clams dug from it as carefully as possible. These were carefully picked over and all stones and shells sorted out. There were then ten pints of clams. Two pints were counted, the first yielding 1,200 clams, the second 1,300. The average of the two pints was therefore 1,250, and the estimate for the clams (ten pints) taken from one square yard is 12,500. In addition to these a considerable number, perhaps a thousand, were lost, being scattered by the tide.

The Rate of Growth.

The rate of growth of the clam, like that of the star-fish, is, under favorable circumstances, more rapid than is usually supposed. It was shown in the last Report that the rate of growth in the star-fish varied greatly according to the amount of food, and that of two healthy star-fishes of the same age one might be more than one hundred times the bulk of the other. The same variation, resulting from differences in food supply, is seen in the clams, though perhaps the difference is not so great.

The growth of the clams, which set thick at Wickford, on Cornelius Island, was followed during the summer, and formed the basis for comparing the growth in other localities. The following figures, photographed life-size, will show the rate of growth of the clams in this locality. Figure 6 represents specimens taken July 7; the larger of these are probably about five or six weeks old, judging from the data with regard to setting already mentioned. Any possible doubt that they are the set of this summer is removed by the fact that a large number of specimens set on the house-boat, which was put into the water on the first of May, were about the same size.

The succeeding figures, from 7 to 14 inclusive, are all life-size photographs of clams taken from the same locality as those in Fig. 6, at various times during the summer. The specimens photographed were selected as representing the average size on each date, together with some of the larger and smaller sizes, placed in the bottom and top row, respectively.

The Rate of Growth Under Special Conditions.—On the sixth of July about a pint of clams, taken from the point already referred to, were placed in a box of sand in the house-boat, and about one-half pint more were added on July 9. The clams were not covered with the sand, but were simply scattered over the surface, many of them sticking together in clumps. In about five minutes they had all burrowed out of sight. The sand box was sunk about 18 inches below the surface of the water, and, not being affected by the rise and fall of the tide, was kept submerged at this depth for a month. During the following month, it was occasionally exposed at low tide when the house-boat was ashore.

The growth of these specimens was compared from time to time with that of the clams in the original locality on the shore, and with the somewhat surprising result that the clams at the house-boat grew much faster than those on the shore, whence the former were originally taken. It is clear, therefore, that it is not necessary for the rapid growth of the young clams that they be in a locality which is exposed at low tide—on the contrary they grow faster when they are submerged all the time. This difference in the growth of the clams on the shore and in the house-boat is illustrated by the photographs of samples taken from two localities at various times. Compare Fig. 9 with Fig. 14; also Figs. 10 and 15; Fig. 11 and Fig. 17; Fig. 12 and Fig. 18.

It might be asked whether the more rapid growth at the house-boat was not due to the more favorable position of the latter in the tide currents. This may be true in some measure, but yet the point of shore in question was washed by a strong current also. The house-boat, moreover, was moored within a few rods of the point, so that the character of the food is about the same. Some other observations confirmed the conclusion that clams grow faster when they are continuously submerged. On September 7, on another part of the shore, the young clams were examined at various levels, from below mean low-water mark to half tide, and the larger growth of the former was noticeable. This is illustrated by samples which were taken at very low tide, and at about half-tide (Figs. 21 and 22).

The following experiment, made to ascertain the rate of growth of individual clams transplanted to another locality on the shore, shows, also, that the growth is greater near the low-water mark. On the 22d of July a number of young clams of average size, taken from the point on Cornelius Island, were carefully measured, and planted in the land tiles. The tiles were set perpendicularly into the ground, and filled with sand taken from *above* tide mark, in order that no clams might be accidentally put into them, and were arranged in a row, from extreme low-water mark to high-water mark, at intervals of about two feet. Each clam was carefully measured and placed in a tile by itself (in some cases two specimens were put into the same tile). On September 18 some of these were taken out and measured again, the rest being left undisturbed. The measurements are of the long diameter of the shell, and are given in millimeters. The accompanying diagram shows the relative position of the tiles which contained the specimens measured on September 18. No. 1 is at extreme low tide, and No. 8 somewhat below half-tide mark.

Number.	July 22.	September 18.	Growth in 2 Months.
(8)	13mm	28mm	15mm
(7)	12 "	36 "	24 "
(6)	14 "	40 "	26 "
(5)			
(4)	11 "	44 "	33 "
(3)	13 "	46 "	33 "
(2)	15 "	48 "	33 "
(1)	13 "	gone.	

Reference to this table shows at once that the clams grow more slowly as we go up the shore from low-water mark. Compare for example Nos. 3 and 8, which at the time of planting were of the same size, but two months afterwards differ 15 millimeters, or more than one-half an inch.

It is not certain, of course, that the difference of rate of growth at different levels is always as marked as in this case, and more experiments must be tried to ascertain the relative growth accurately. This experiment, so far as it goes, substantiates the conclusion already stated that clams grow faster when they are under water the greater part of the time. The reason for this is not very far to seek. The food of the clams consists of microscopic organisms contained in the water, which is taken in through one siphon and expelled through the other. The clams can feed, therefore, only when covered by water, and those which are located at some distance above the low-water mark are shut off from the food supply during a considerable portion of each day.*

This record of growth of the clams in the tiles is interesting also because it demonstrates that clams may grow during their first summer nearly to marketable size. The specimen in tile No. 2 was not among the very largest of the set on the point at the time it was transplanted, and not larger than some of those which had set in the floating house-boat; so that there is no question about it being of this year's production. On July 22 it measured 15 millimeters—the size of the specimen in Fig. 20. On September 18, in less than two months, it had more than trebled its length and had burrowed about six inches into the sand. The specimen was preserved on September 18 and is photographed natural size in Fig. 20 by the side of a clam of fifteen millimeters in length. The growth of the two adjacent specimens in the tiles Nos. 3 and

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*Since the rapidity of growth of the clams depends directly upon the supply of microscopic organisms in the water, it is to be expected that a considerably greater growth will be found in some portions of the Bay than in others. I have not had an opportunity to investigate this problem carefully, but through the kindness of Mr. A. W. Bourne some samples of this year's clams were obtained on December 5 which were much larger than those taken at the same time at Wickford. The water in the former locality is extremely rich in microscopic organsims, shown both in the skimmings taken with a tow-net and by the remarkable growth of animals other than clams which depend upon these organisms for food.

4 indicates that the record for the specimen photographed is not exceptional or accidental.

Another experiment made to ascertain the rate of growth of individual clams was tried at the house-boat. On July 19 several specimens were carefully measured and placed in small flower-pots which were filled with sand. These were kept continuously under water, and the clams measured again on September 10. The measurements on the two dates, as given below, show that the clams had grown during seven and a half weeks to two or three times their original length.

Record of Growth of Clams in Pots at House-Boat.

Number.	July 19.	September 10.
(1)	11–11 (2 specimens).	26–23
(2)	9.2	22
(3)	7.5	—
(4)	8.1	27
(5)	12.5	28
(6)	10.9	30
(7)	11.1	25
(8)	8.9	30
(9)	10.5	22 (shell only).
(10)	11.5	20 (shell only).
(11)	11.1	27
(12)	9.0	26

The following will give an idea of the relative increase in bulk of the clams at the house-boat as compared with those on the shore. On August 9 the clams on the point of shore to which we have several times referred were measured by the pint and counted. The average number to the pint was about 1,200. The clams which were taken from the same locality on July 7 and 9, and which had been kept in a box of sand at the house-boat since that date, now measured about 400 to the pint. The clams at the house-boat, therefore, appeared to have so far outstripped those on the shore that in one month they became about three times the bulk of the latter. There is one possible fact, however, which may make this result less trustworthy than the data derived from the growth of marked individuals or from that of the largest specimens in each locality, viz.: the clams which were placed in the house-boat were gathered with a sieve, which, though its meshes were small (ordinary flour-sieve), may have allowed many of the smaller clams to go through; so that the average size of those planted was perhaps less than the average size of those remaining on the shore.

The actual increase in bulk of a certain quantity of clams during ten weeks in the summer is given in the following measurement of the clams reared in the house-boat. The box of sand in which a pint and a half of small clams was planted as evenly as possible, on July 6–9, was divided in the middle by a partition. The clams soon became so crowded that many were probably pushed out; at any rate there was a considerable number of empty shells over the surface of the sand. Notwithstanding this loss, four and a half quarts were taken from one-half of the box on September 18, the other half being left undisturbed. From about three-fourths of a pint, therefore, we had a yield of over four quarts of clams in about ten weeks. We ought also to mention that one pint was taken from the box on August 5, and smaller quantities on several other occasions.

Size and Age at Sexual Maturity.

It is usually maintained that the clam reaches sexual maturity during the third year of its life,* but I am inclined to believe that this does not do justice to the animal in question, and that the clam, like the star-fish, not only grows faster, but arrives at sexual maturity much sooner than is usually supposed. My reasons are as follows :—

1. I found at the beginning of the breeding-season a ripe male

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* See Bulletin 51, R. I. College of Agriculture and Mechanic Arts, December, 1898.

clam of 30 millimeters in length, and a ripe female of 50 millimeters. As we have already stated, many clams, undoubtedly of this year's growth, were more than 30 millimeters long, and some nearly 50 millimeters, before the end of September.

2. In the autumn the sexual glands of this season's clams were considerably developed, although the breeding-season does not occur until spring.

Therefore, while I cannot make it as a positive statement, not having yet followed the development of the sexual glands throughout the year, I would venture the conjecture that many of the clams of last summer's set (1899) will breed next spring (1900).

Summary of Preceding Chapters, and Bearing of These Results on the Problem of Clam Culture in Narragansett Bay.

(1) From the point of view of clam culture, and the practicability and feasibility of re-instating an almost defunct industry, the observations recorded in the preceding pages open up a very encouraging prospect.

(2) The preliminary survey indicates that there are more than fifty miles of Rhode Island shore in the Bay alone which are more or less available for the rearing of clams.

(3) The range and the adaptability of the clam is great. It will thrive in various kinds of soil; in sand, mud, clay, and among stones; from near high-water to considerably below low water; from brackish ponds to the densely salt water of the outside shore and Seaconnet river.

(4) It is the general testimony that the clams have been decreasing in quantity gradually during the last twenty years, and it is an undisputed fact that they are now comparatively scarce. The disappearance has been nearly uniform in all parts of the Rhode Island shore of the Bay; in localities protected from the wash of the steamers and not contaminated by the waste of towns, as well as in localities less fortunately situated. It is still, in certain localities, comparatively abundant below the low-tide mark,

where it cannot be taken by the ordinary method of digging, but only by the more elaborate and unusual method of churning. In Cole's river, where, under Massachusetts laws the clams are better protected, they are much more abundant than in the neighboring Rhode Island estuary, Kickemuit river, though both are similarly situated and the latter has been proved by its past history to be a locality as favorable as the other. These facts and others indicate clearly that the decrease in the clams of the State is due mainly to the unlimited and promiscuous digging and not to changed natural conditions.

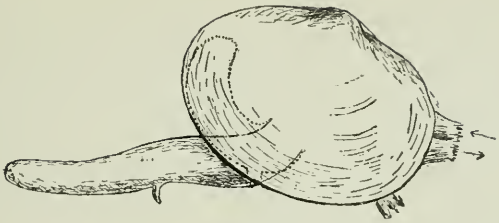
(5) That frequent digging up of the ground is necessary, or that it is even a positive benefit to the clams, by rendering the ground soft, is probably a fallacy. The fact that often the finest specimens are found in hard, stony ground, or in hard clay flats, which are only occasionally exposed to the clam-digger at an unusually low tide, and the observations made during the summer upon the growth of unmolested specimens, indicate that they grow well, at any rate, if left undisturbed. The habits of the animal, in obtaining food, point to the same conclusion. The food is obtained from the water which is taken in through the siphon, and not from the soil in which the clam lies. So long as it is well located, therefore, and in communication with the water it is distinctly not to its advantage to be disturbed, particularly at the risk of being buried deep under the mud or left on the surface, a prey to crabs, mummichogs, star-fish, and other enemies. Clams less than one-half an inch long will burrow very rapidly when they are exposed on the surface of the mud (if covered by water), but those upwards of three-fourths of an inch will often lie for a long time without even trying to burrow, and then are not very efficient in getting into the mud. This method of "cultivation," although undoubtedly excellent for apple trees, is not, however, equally good for clams.

(6) The breeding-season of the clam is at its height in June. The exact limits of the period have not been ascertained. The eggs are extruded in great numbers into the sea-water where they

are fertilized and in a short time develop into very minute free-swimming forms with little resemblance to the adults. In this condition they live an active life and are carried hither and thither by the tides for several days at least before they settle down to the bottom or attach themselves to some object like a stone or piece of sea-weed. The obvious result of this method of reproduction is that the young clams do not remain where the eggs are laid but are very widely distributed by the tides. This fact readily explains the sudden appearance of a large set of clams in a locality where the adults are scarce. It is not at all unlikely, moreover, that the clams below tide-mark, and out of reach of their human enemy, produce a large proportion of the clams which set on the shore. (See foot-note, p. 15.)

(7) In the manner of setting, and in the peculiar characteristics of the young clams after they have set, there are two facts which will prove of the greatest service in clam culture. 1. The clam set is not evenly distributed even in regions of the Bay where the water is full of the free-swimming young, but in some localities the set is extremely thick while in neighboring localities, a few rods distant, only a small number may be found. 2. The young clams, from one-fourth to one-half an inch long, have a remarkable capacity for burrowing, a capacity which is greatly diminished as the animal grows larger. At the proper season, therefore, and in the localities where the set is thick, the clams can easily be collected in immense numbers by means of a sieve; and fortunately the time when they can be collected with the least difficulty happens to be the very best time for transplanting. By far the best time for collecting and transplanting is from the first week in July to the first or second week in August. It is hundreds of times easier to collect them at this season by means of a sieve than at other times of the year with a clam-hoe. There is perhaps even a greater advantage in transplanting at this time, from the fact that the clams can now be sowed broadcast like grain and will soon burrow into the sand; whereas, larger specimens from one inch upwards must necessarily be planted and carefully covered

PLATE I.



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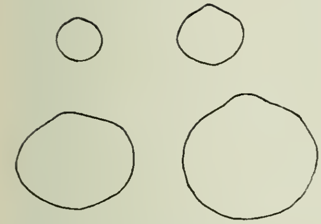

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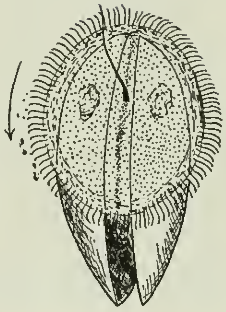

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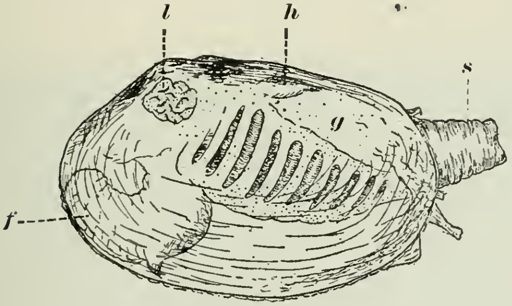

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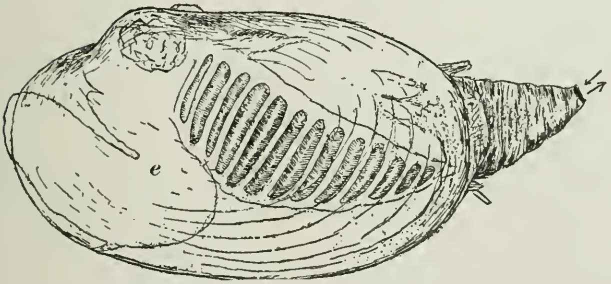

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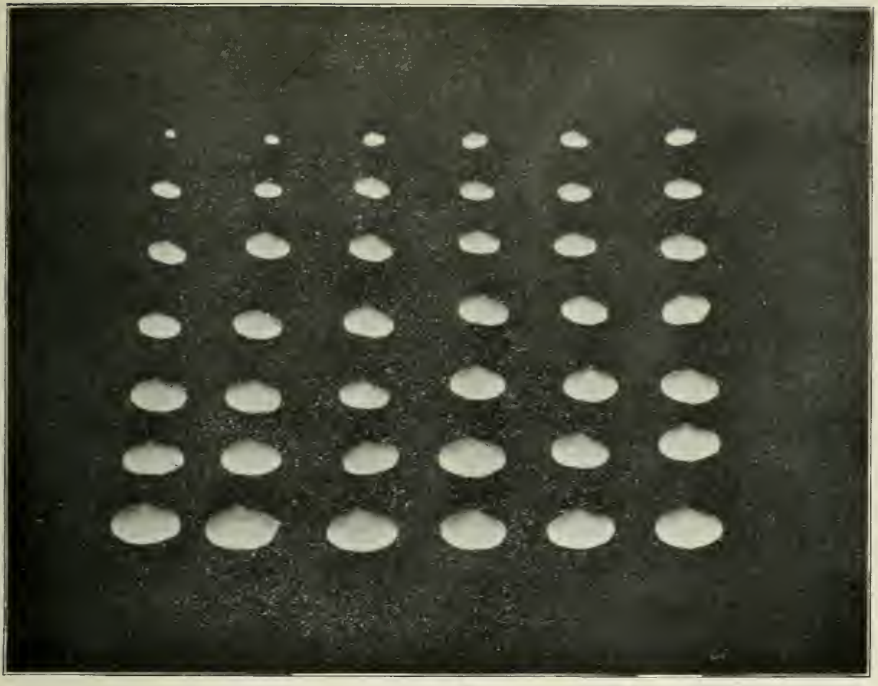

FIG. 6.

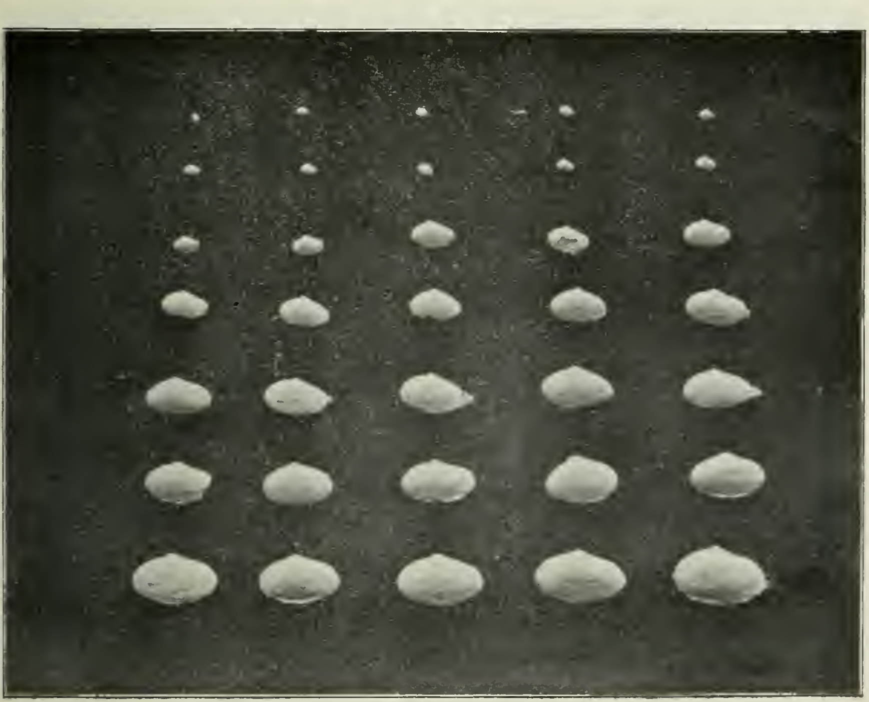

FIG. 7.

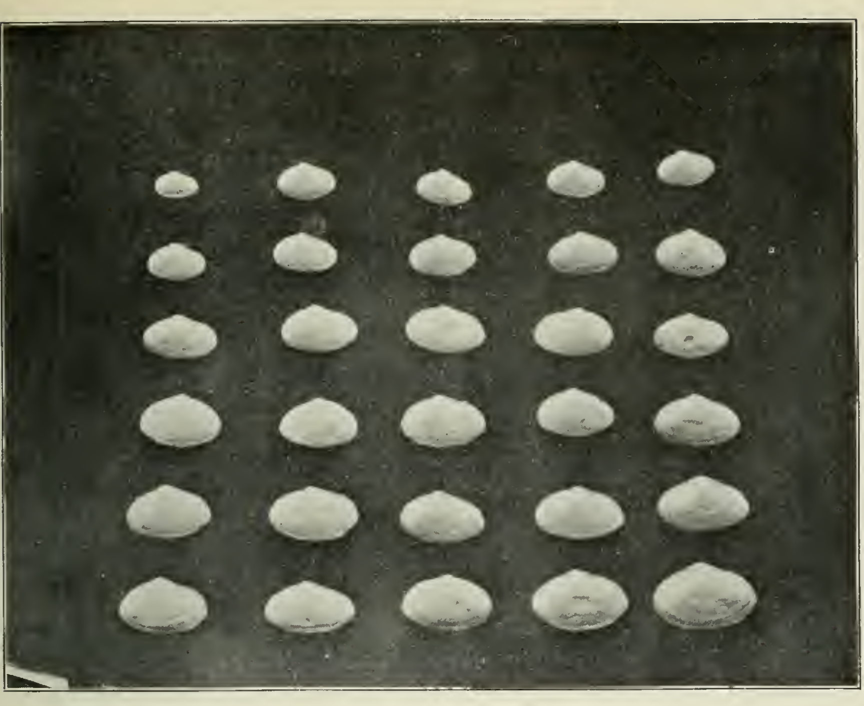

Fig. 8.

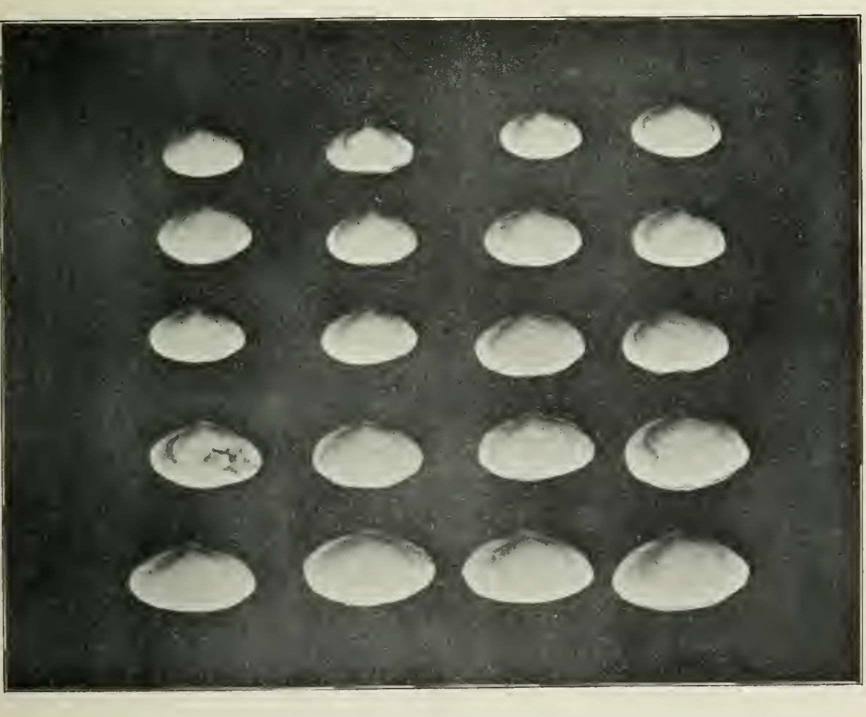

Fig. 9.

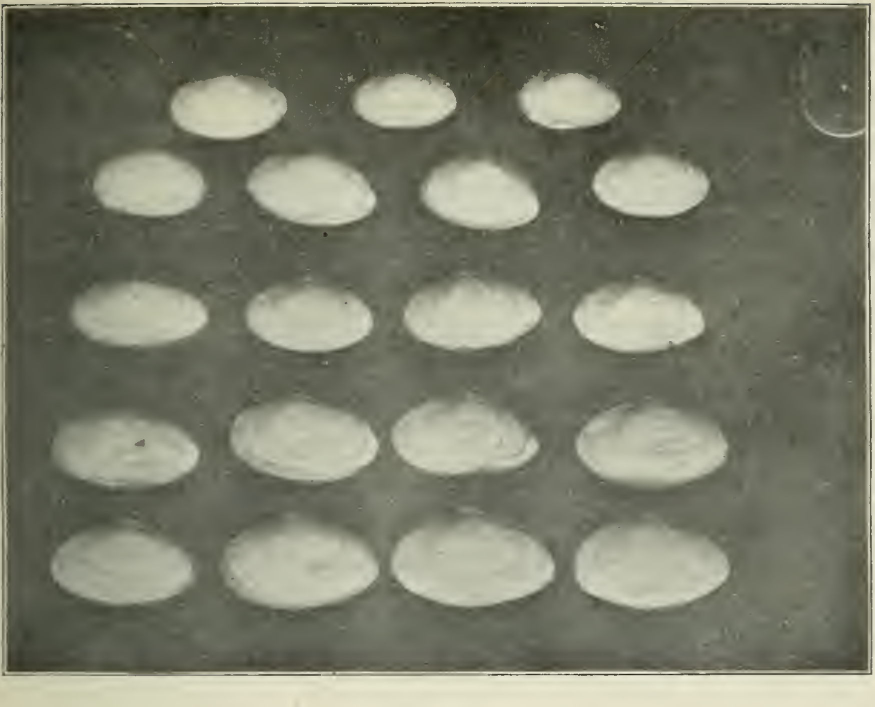

Fig. 10.

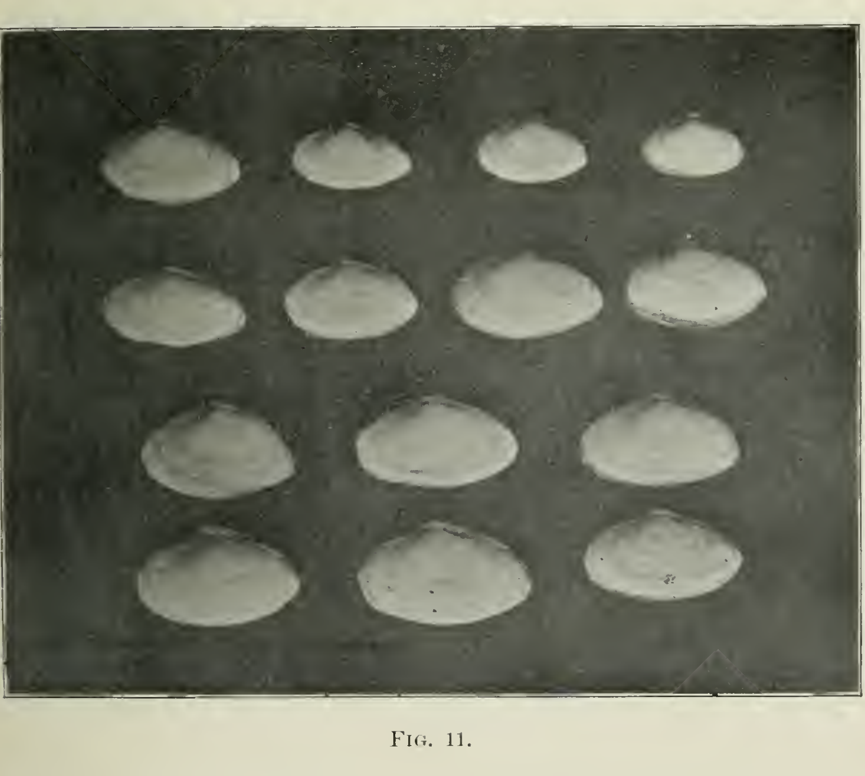

Fig. 11.

PLATE V.

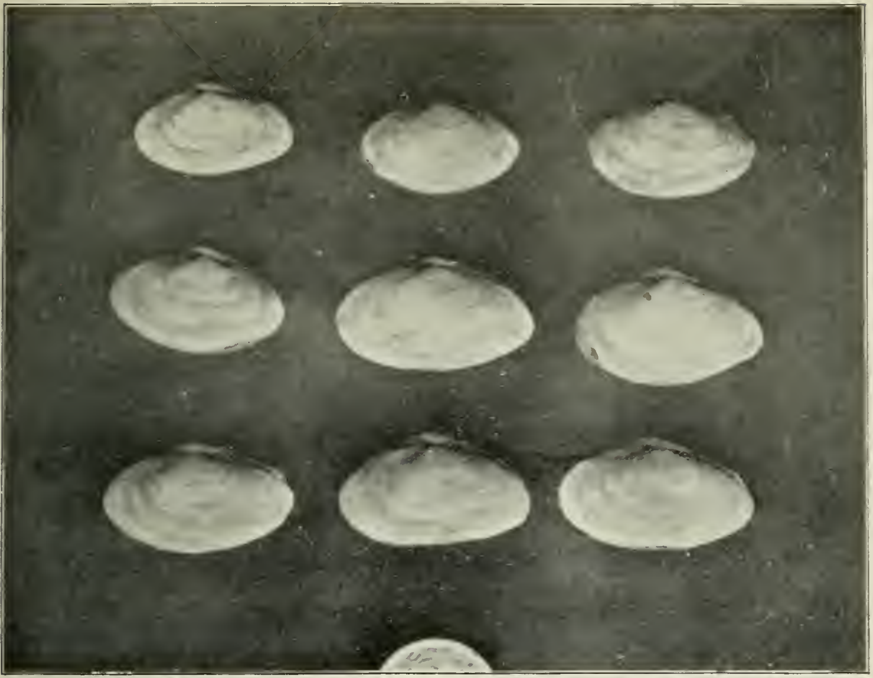

FIG. 12.

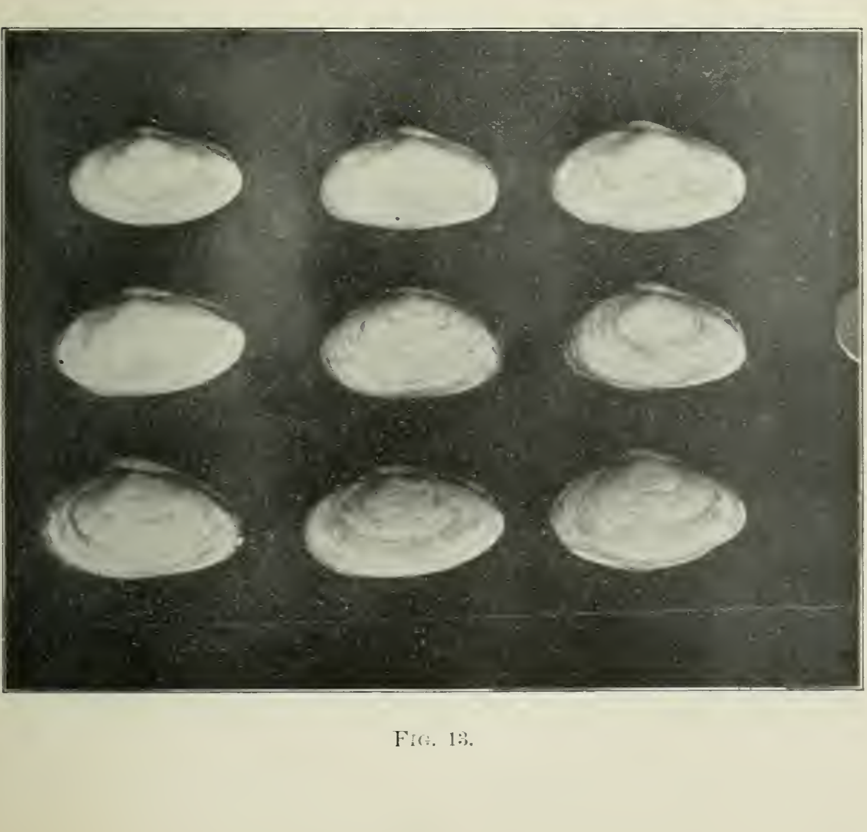

FIG. 13.

PLATE V.

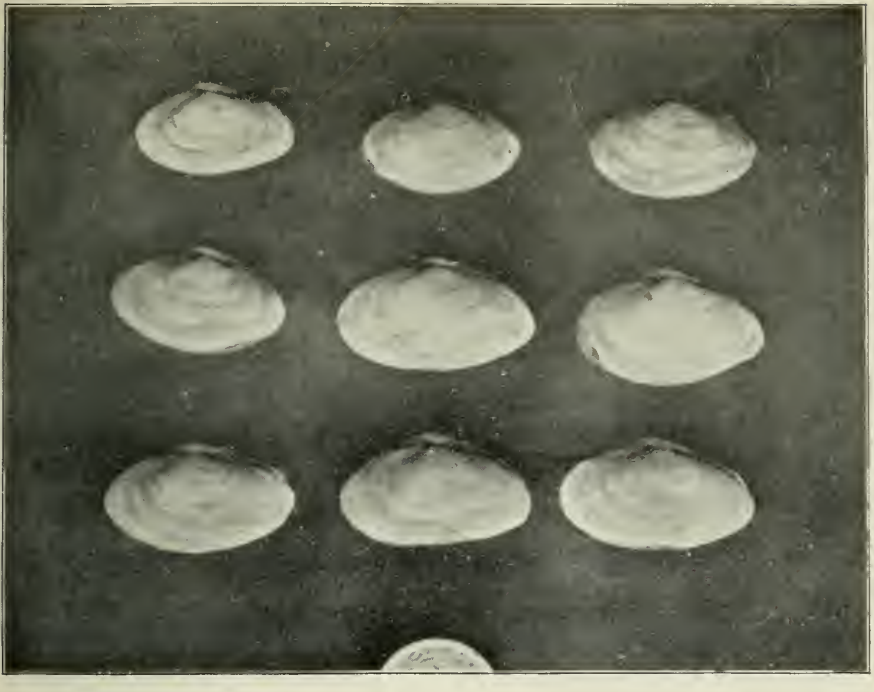

FIG. 12.

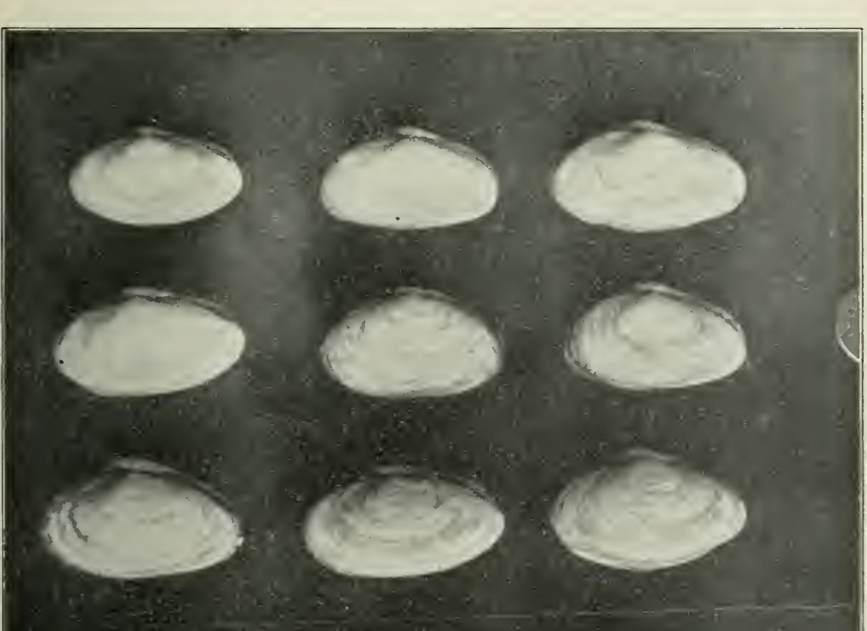

FIG. 13.

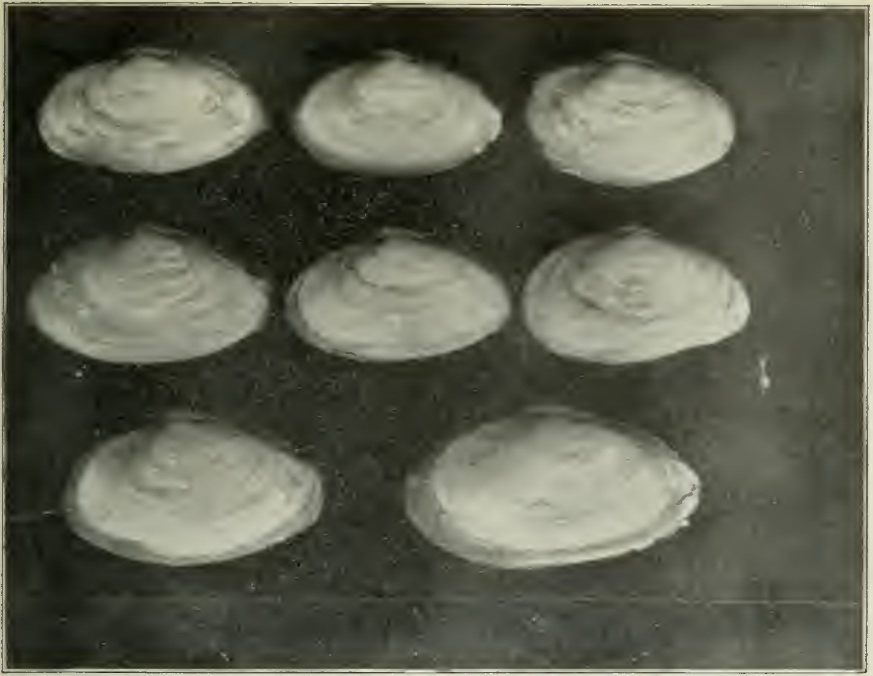

Fig. 14.

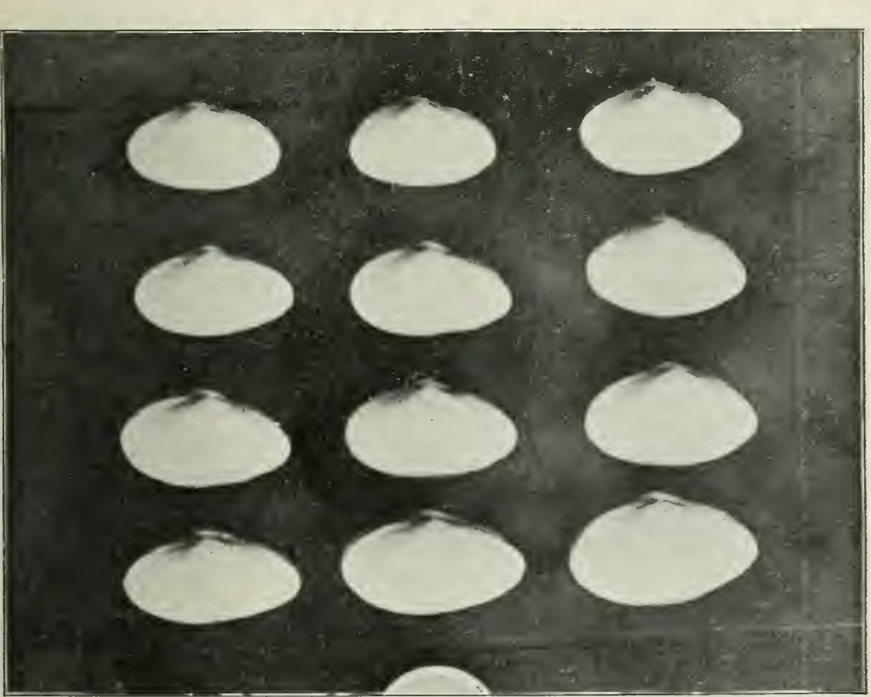

Fig. 15.

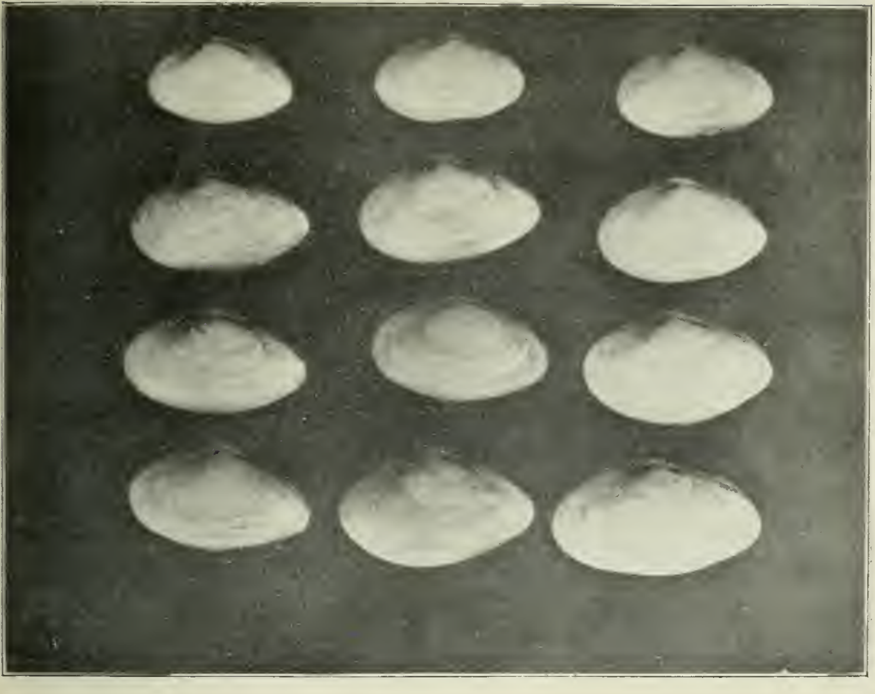

FIG. 16.

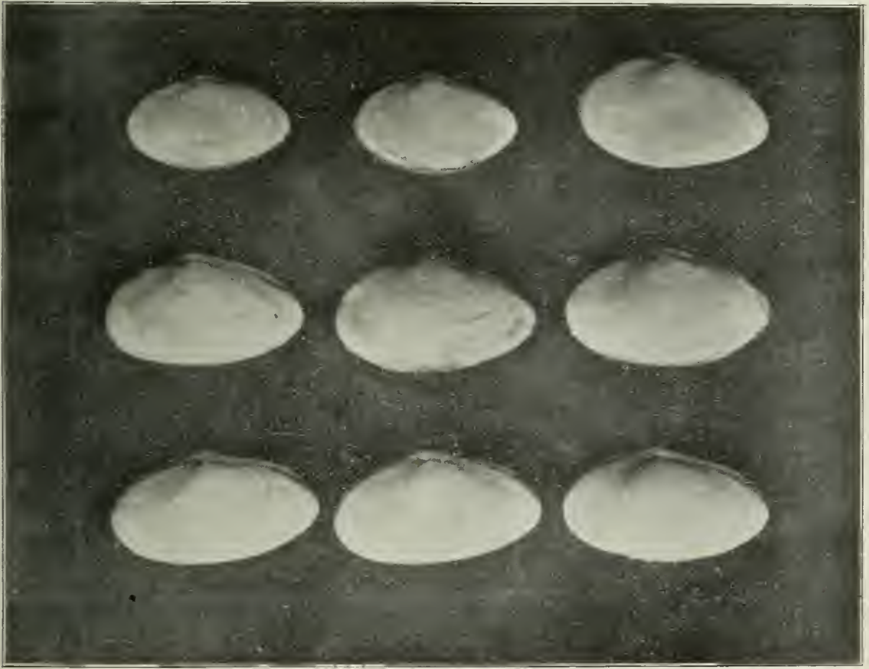

FIG. 17.

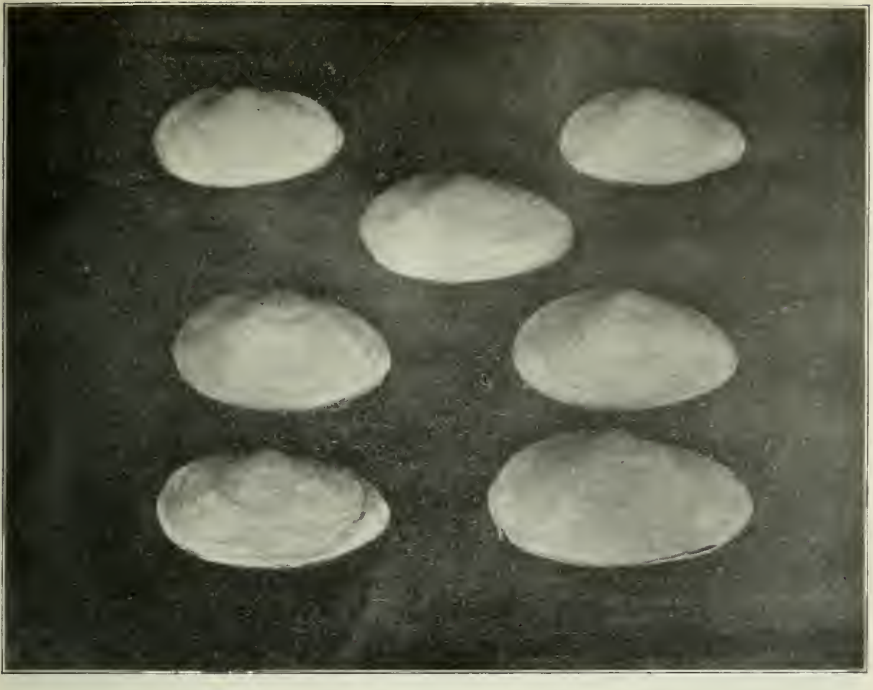

FIG. 18.

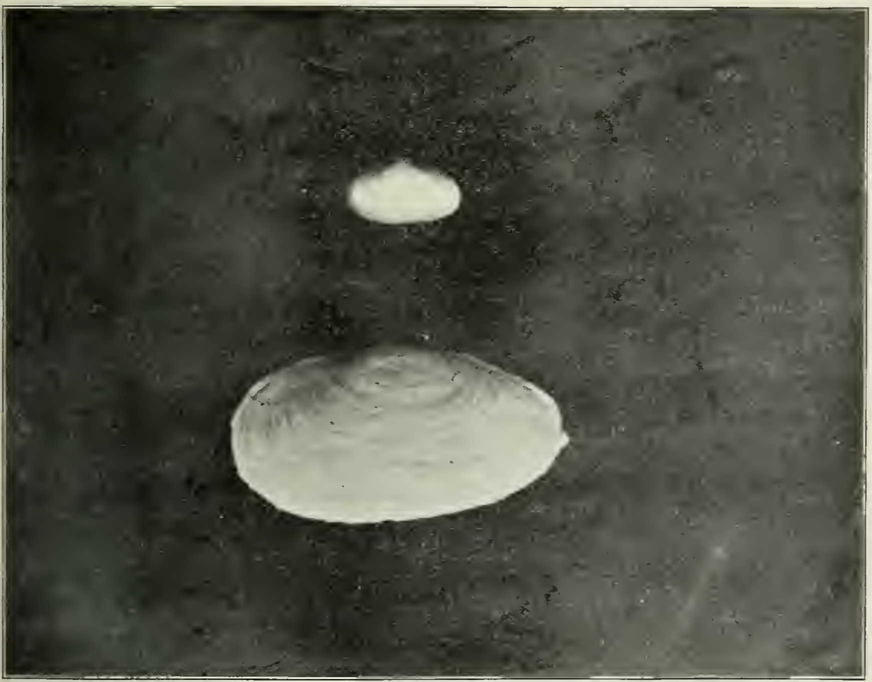

FIG. 19.

PLATE IX.

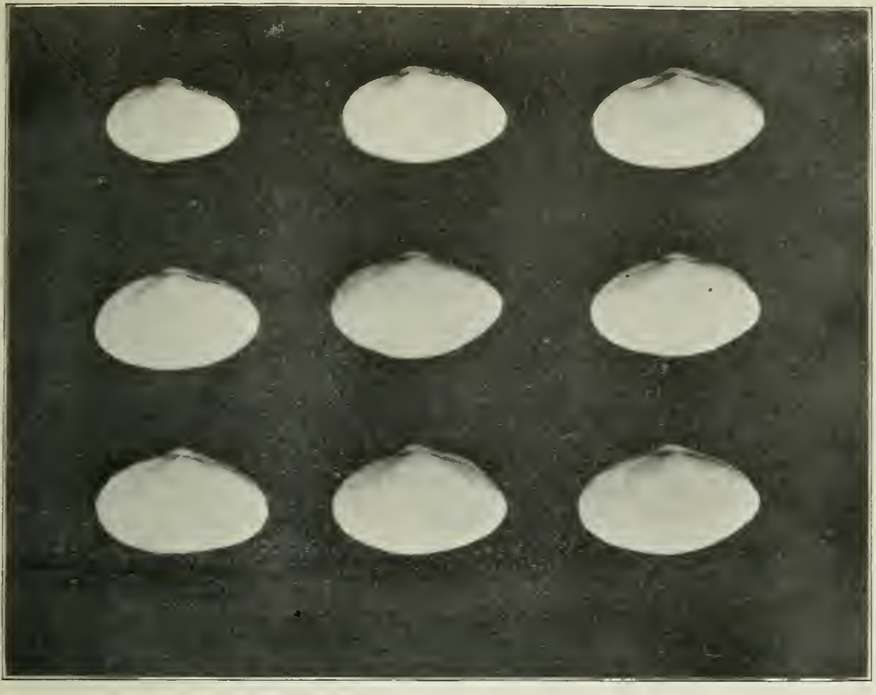

FIG. 20.

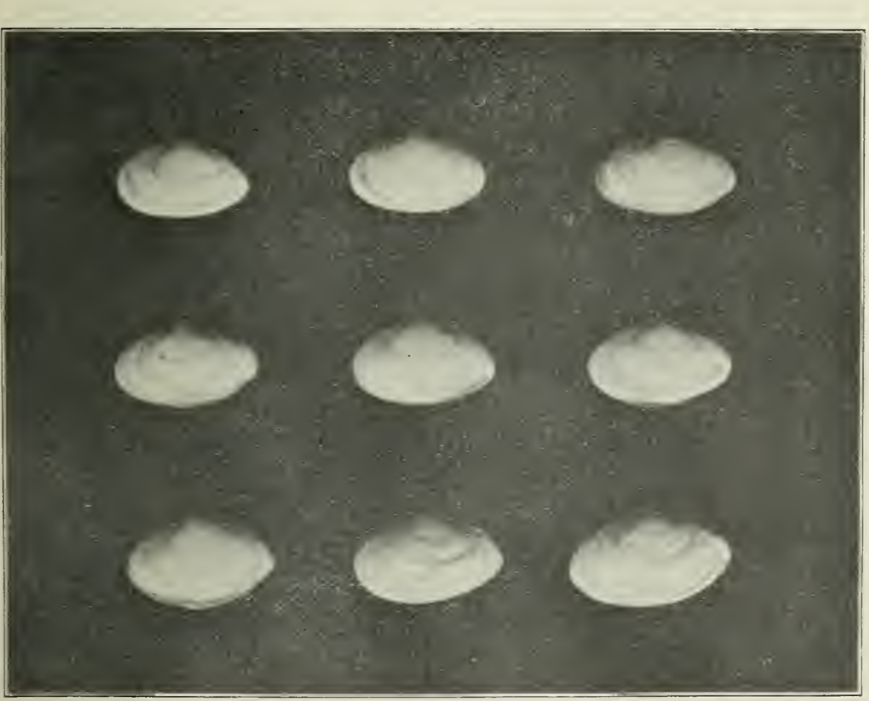

FIG. 21.

Plate X.

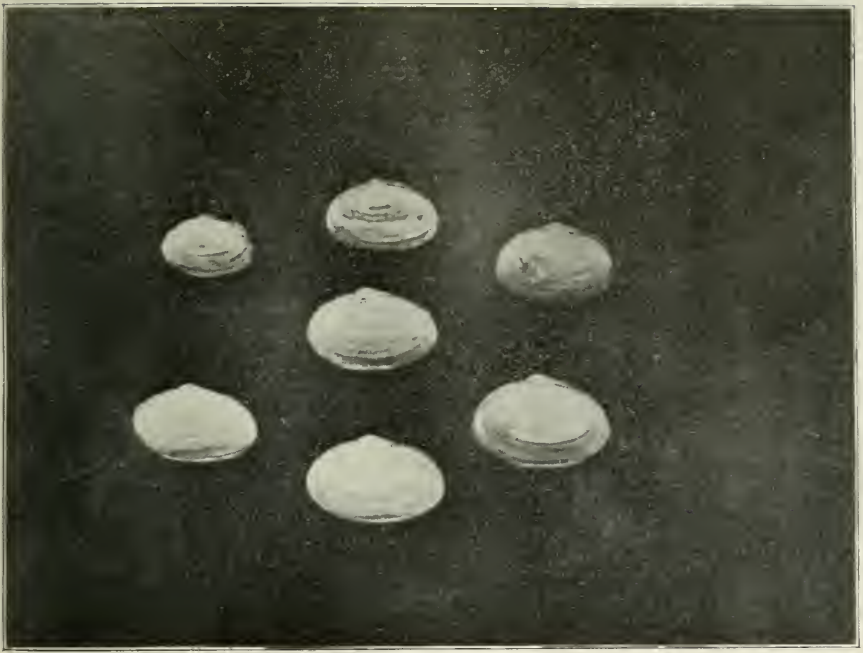

Fig. 22.

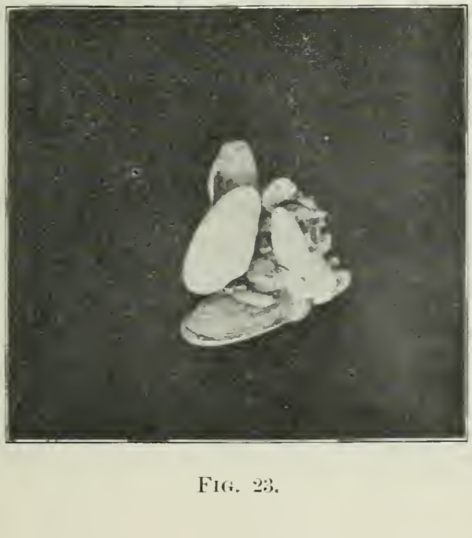

Fig. 23.

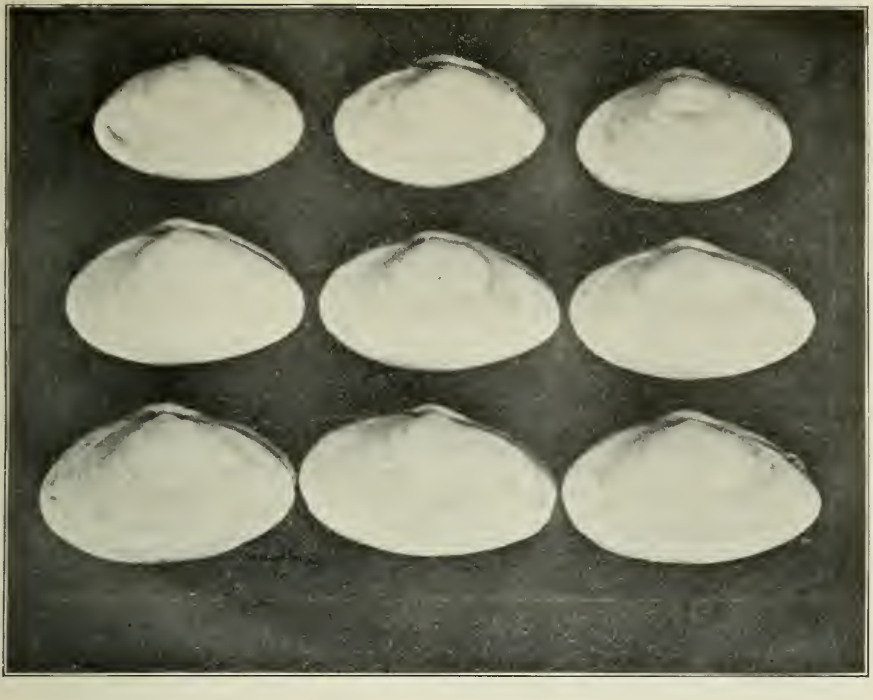

FIG. 24.

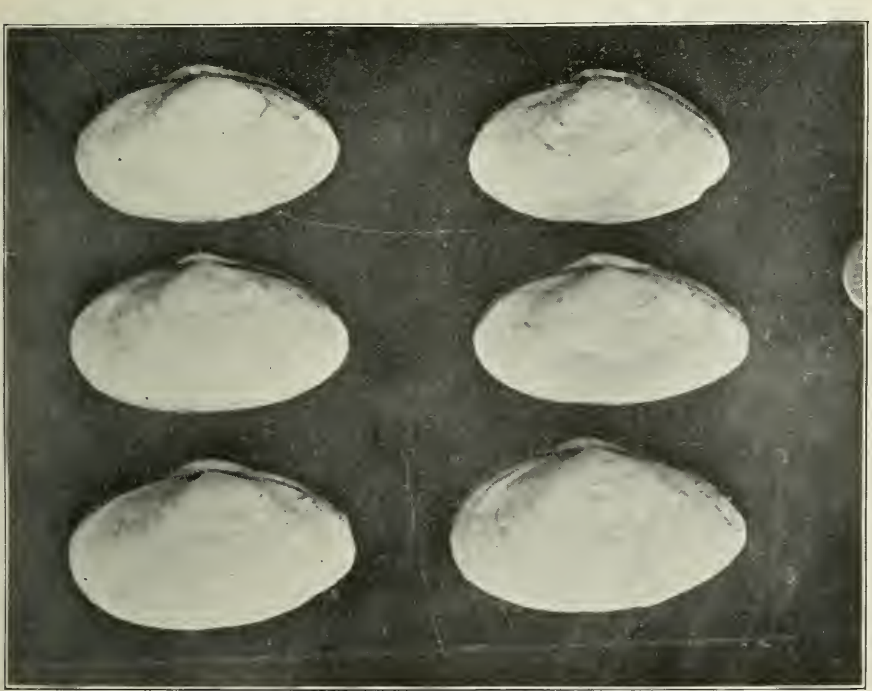

FIG. 25.

or a great loss will result. An additional fact in favor of transplanting at this time is that in some localities there are very great quantities of young clams set early in July which, if not taken up and transplanted, are destroyed by shifting sand or from some other cause. In other localities the clams are set too thick to grow to the best advantage, and they would actually be benefited by being thinned out.

(8) It seems almost certain that the explanation of the abundant set in a limited area, and the meagre set in the neighboring localities, is to be sought in the position of the shore with reference to the tides. When this explanation has been worked out in detail it may be possible artificially to construct and place apparatus to collect the set in equally large quantities.

(9) The experiments of transplanting have demonstrated that under favorable conditions the rate of growth is more rapid than is usually supposed, some of this year's set having reached a length of nearly two inches by the middle of September. The experiments demonstrate also, the fact that there are great differences in the rate of growth according to the food supply which is obtained from the water, and that the most rapid growth may be expected of clams which are under water most of the time.

(10) The size and age at which the clams reach sexual maturity has not been definitely ascertained, but there are facts which indicate strongly that they breed during the first year of their life. It has elsewhere been stated that they do not breed until the third year. The question is important, of course, in view of any attempt at clam culture on a large scale or at restocking the shores.

EXPLANATION OF FIGURES.

1. Sketches, drawn with camera lucida, of young, free-swimming clams, showing shape and variation in size.

2. Camera drawing made on June 14 of a clam caught in the skim-net at the surface of the water on May 29, and kept isola-

ted in a dish of water. Seen from the left side: f, foot retracted; l, liver; h, heart; g, gills; s, siphon or "snout." Arrows indicate incurrent and excurrent openings.

3. The same individual as Fig. 2, drawn to the same scale of magnification, ten days later, viz.: on June 24; e, sense organ (ear?). Other letters the same as Fig. 2.

4. Freehand sketch of clam larva seen through the microscope with swimming-organ (velum) expanded. Around the edge of the velum is the fringe of minute lashes (cilia) whose movements propel the animal. The arrow shows the direction of the current of water created by the rapid stroke of the cilia. The direction of the current is easily ascertained by observing the movement of the small particles contained in the water.

5. Sketch of a clam just set, as seen under the microscope. The large foot and the siphon are shown distended. The dotted line indicates the position of the foot when retracted within the shell. The incurrent and excurrent tubes of the siphon are, at this stage, nearly separate.

6. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on July 7, 1899. The largest specimens are, probably, about six weeks old. Photograph life-size.

7. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on July 14, 1899. The largest specimens are, probably, about seven weeks old. Photograph life-size.

8. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on July 21, 1899. The largest specimens are, probably, about eight weeks old. Photograph life-size.

9. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wick-

ford, R. I., on August 4, 1899. The largest specimens are, probably, about ten weeks old. Photograph life-size.

10. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on August 29, 1899. The largest specimens are, probably, about thirteen weeks old. Photograph life-size.

11. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on September 7, 1899. The largest specimens are, probably, about fourteen weeks old. Photograph life-size.

12. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on September 30, 1899. The largest specimens are, probably, about four months old. Photograph life-size.

13. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on December 4, 1899. The largest specimens are, probably, about six months old. Photograph life-size.

14. Specimens selected to represent the average size of the clams in a marked area on the shore of Cornelius Island, Wickford, R. I., on December 4, 1899. The largest specimens are, probably, about six months old. Photograph life-size.

15. Specimens selected to represent the average size of clams taken on July 7, 1899, from a marked area on Cornelius Island, Wickford, R. I., and reared in a sand-box at the house-boat until August 8. These specimens are, probably, about ten and a half weeks old. Compare with those remaining on the shore until August 4. Photograph life-size.

16. Specimens selected to represent the average size of clams taken on July 7, 1899, from a marked area on Cornelius Island, Wickford, R. I., and reared in a sand-box at the house-boat until August 29. These specimens are, probably, about thirteen weeks

old. Compare with those remaining on the shore until August 29. Photograph life-size.

17. Specimens selected to represent the average size of clams taken on July 7, 1899, from a marked area on Cornelius Island, Wickford, R. I., and reared in a sand-box at the house-boat until September 8. These specimens are, probably, about fourteen weeks old. Compare with those remaining on the shore until September 7. Photograph life-size.

18. Specimens selected to represent the average size of clams taken on July 7, 1899, from a marked area on Cornelius Island, Wickford, R. I., and reared in a sand-box at the house-boat until September 19. These specimens are, probably, about sixteen weeks old. Compare with those remaining on the shore until September 30. Photograph life-size.

19. The large specimen was taken on September 18 from a land-tile set in the mud on the shore (Wickford), at low-water mark. It was placed in the land-tile on July 22, when it was the size of the smaller specimen. The difference in size represents two months' growth. Photograph life-size.

20. These specimens represent the average size of the larger of the clams at low-water mark in a certain locality on the shore at Wickford on September 7. (Compare with those from the same locality at *half-tide* mark.) Photograph life-size.

21. These specimens represent the average size of the larger clams at half-tide mark in a certain locality at Wickford on September 7. (Compare with those from the same locality at *low-water* mark.)

22. These specimens were found among the barnacles clinging to the outside of the house-boat on September 7. They have never been covered with sand or soil of any kind, and are stubby and thick-shelled. Photograph life-size.

23. These specimens were taken on September 7, from the side of the sand-box in the house-boat, and show how the clams of considerable size may remain anchored to various objects, or

to each other, so as to form clumps, like mussels. Photograph life-size.

24. These specimens represent the average (smaller) size of clams taken from the shore in the Kickemuit River on December 4. They are about six months old. Photograph life-size.

25. These specimens represent the average (larger) size of clams taken from the shore in the Kickemuit River on December 4. They are about six months old. Photograph life-size. Compare with those taken at Wickford, on shore, at the same date.

ON THE CORRELATION BETWEEN GROWTH AND FOOD SUPPLY IN STARFISH.

By A. D. MEAD.

American Naturalist, Vol. XXXIV, No. 397, January, 1900.

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WIDEST SENSE

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1900

ON THE CORRELATION BETWEEN GROWTH AND FOOD SUPPLY IN STARFISH.

A. D. MEAD.

In the higher vertebrates there is a pretty constant relation between the age of an individual and its size, at least up to the time when the full stature is reached. This relation is expressed in carefully constructed curves of growth, and it may be inferred from common observation. The healthy individual must be able, during its early life, not only to hold its own in respect to size, but also to grow; the time between meals must be comparatively short, and the nourishment assimilated must be more than sufficient merely to replenish waste tissue. Minot has shown for guinea pigs that even "any irregularity in the growth of an individual tends to be followed by an opposite compensating irregularity." "If an individual grows for a period exceedingly fast, there immediately follows a period of slower growth; and, *vice versa*, those that remain behind for a time, if they remain in good health, make up the loss (at least in great part if not always completely) soon after." "Each individual appears to be striving to reach a particular size" — a particular size, we might add, not only for the adult age but for any particular previous age.

The normal rate of growth of marine invertebrates seems not to have received much attention, and were one to inquire among longshoremen or seaside naturalists how old an eight-inch lobster is, or how long it takes a starfish to grow to a certain size or to become sexually mature, he would meet with an interesting variety of opinions and receive little satisfactory information.

Several years ago Alexander Agassiz made an estimate of the rate of growth in starfishes, which was based upon the supposition that a close relation does obtain between size and age in these animals as well as in vertebrates. The method which he employed was previously used by the elder Agassiz for ascertaining the age of many marine animals (*Proc. Essex Inst.*, 1863), and is explained in the following quotation from the monograph on North American starfishes:

"The young starfishes figured on this plate (Pl. VIII) were all found attached to roots of Laminaria thrown up on the beaches in the neighborhood after a storm; and from their different stages of growth, as compared with the oldest starfish raised from a brachiolarian (Pl. VI, Fig. 11), specimens of which were also found upon these roots, it is probable that the sizes here figured are one (Fig. 1), two (Fig. 8), and three (Fig. 10) years old. A considerable number of specimens were picked up in this way, and they could all be arranged into very distinct groups, representing the starfishes of the present and two previous seasons. There seemed to be no gradation from one group to another, such as we have among the young sea urchins, which, in consequence of their manner of breeding during the whole year, form series the relations of which it is impossible to determine. In this connection I would say that, by arranging the starfishes found upon our rocks into series according to their size, we are able to obtain a rough estimate of the number of years required by them to attain their full development; this I presume to be somewhere about fourteen years. They begin to spawn before that time, as specimens have been successfully fecundated which evidently were not more than six or seven years old."

During the summer of 1898 the writer had an excellent opportunity to study the rate of growth of the starfish (*Asterias forbesii*) at a floating laboratory moored in one of the estuaries of Narragansett Bay. The breeding season was short and definite, and the larvæ began to "set" the last of June.

On June 29, innumerable young starfish, about as large as the head of a pin, were discovered clinging to the eelgrass and to the rockweed and other algæ, where a few days before none could be found. A handful of the fluffy seaweed, *Heteromorpha*, bespangled with minute stars, was placed in a floating car, whose sides were encrusted with a young growth of barnacles, fresh fronds of green algæ, and delicate branching stalks of hydroids. That the little starfish found here a natural and congenial environment was evident from their healthy appearance, their quick response, and their rapid growth.

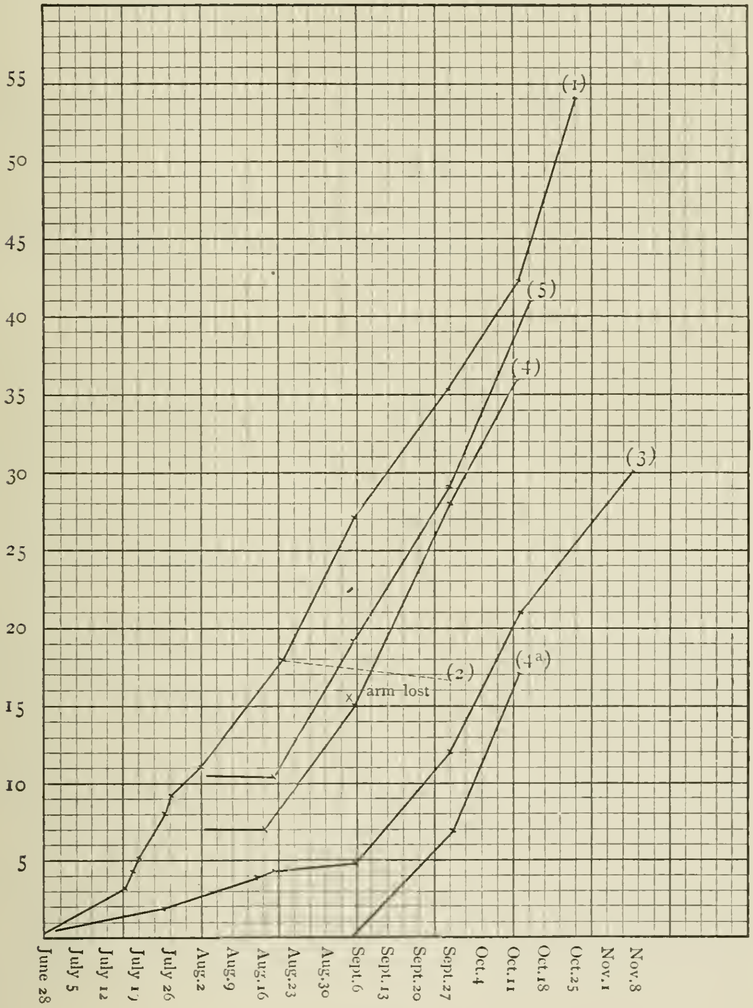


Fig. 1.

They were kept under observation until November and fed on barnacles, small clams, and mussels. As they were examined from time to time, two features of their growth were especially noteworthy, *viz.*, its rapidity and the difference in rate in different individuals. On June 29 none of the stars measured more than 1 mm.;[1] on July 18 one of the larger specimens measured 5 mm.; July 26, 9 mm.; August 18, 18 mm.; September 26, 35 mm.; October 25, 54 mm. (over 2 inches). Curve 1, Fig. 1, is a graphic representation of the growth of these stars and is constructed from measurements of the largest specimens which could be found in the car at each observation. At any time after the first few weeks some of the specimens were three times as large as others, and between these all intermediate stages could be found. On August 18, for instance, eight specimens, arranged according to their sizes, measured 7½, 8½, 10½, 12, 13, 14½, 16, and 18 mm. A similar series — or a more perfect one — might at any time be arranged from specimens taken along the shores.

From the fact that in starfish of the same age such great differences in size exist, with all gradations between the extremes, it is evident that there is danger in applying to them Agassiz's method of ascertaining age. Indeed, the specimens which were calculated by him to be three years old were not one-fifth as large — linear measurement — as those known by actual observation to be only three months old.

Coming now to the consideration of the conditions which determine the *difference* in the rate of growth in these animals, we may exclude certain factors at once; for example, the influence of light, temperature and density of the water, and size of containing vessel, inasmuch as these conditions are practically the same for all the individuals under observation.

It appears from some other experiments, however, that difference in the amount of food is the principal, if not the only, factor. The starfish differs from the higher animals in this important respect; it can eat and *assimilate* many times as much food as is necessary merely to maintain a healthy condition. When food is accessible, the starfish eats voraciously and grows with great rapidity; but, on the other hand, it will live for months almost without food and apparently remain healthy, though it does not grow. As one watches a large number of stars of the same age and size, transferred to a new car, he will not fail to notice that some of them happen upon a favorable food supply before the others, and in consequence grow at first much faster than the rest. Then, not only do these larger specimens have the better chance of getting food, but, if the animals usually preyed upon become scarce, the larger starfish do not hesitate to devour the smaller ones. It was noticed repeatedly that the variation in the rate of growth was much greater among the starfish whose food supply was limited than among those abundantly provided for. The immediate effect upon the rate of growth of the supplying and the withholding of food is demonstrated in the following experiments.

---

[1] All the measurements given below as "length" are from the mouth to tip of arm.

One of the starfishes in the car which had grown most rapidly up to August 18, when it measured 18 mm. (see curve 1), was kept until September 26 with very little to eat. During these five weeks there was no growth in this specimen (curve 2), but rather a slight decrease, although the largest specimen left in the car had doubled its length.

Another small starfish (curve 3), which was caught in the tow net as a brachiolarian and "set" in the aquarium on June 28, was kept on a very small allowance of food until July 23, when it measured 2 mm. It was then fed occasionally on small barnacles, and on September 6 measured 5 mm. After this it was given an abundance of food, with the following result: September 26, 12 mm.; October 12, 21 mm.; November 5, 30 mm.

Several other starfish which were caught in the tow and set in an aquarium at the same time with the last were kept on a small allowance until September 6, and were then apparently in good health, although they had grown but little. Fig. 2 *A* represents one of these at the age of about five weeks, and Fig. 2 *B* represents a well-nourished specimen of the same age, taken from the car.

Two specimens (curves 4, 5) of medium size, 7 mm. and 10½ mm., respectively, were transferred, on August 3, from the original car, where they had been reared on barnacles, to an adjacent car. They were supplied with a bunch of small mussels, which, however, the starfish could not or would not open, and on August 16, after a period of thirteen days, they had not grown at all. From this time they were provided with an abundance of their usual food — barnacles — and grew with great rapidity, as is indicated in the curves. On November 12 they measured, respectively, 36 and 41 mm.

Incidentally curve 4 shows another interesting point, namely, that the loss of an arm does not cause a diminution in the rate of growth. On September 5 an arm was accidentally torn off, yet the rate of growth of the rest of the body was as rapid as before, and as rapid as that of the other starfish (curve 5). The rate of growth in the regenerating member is indicated in curve 4 *a*.

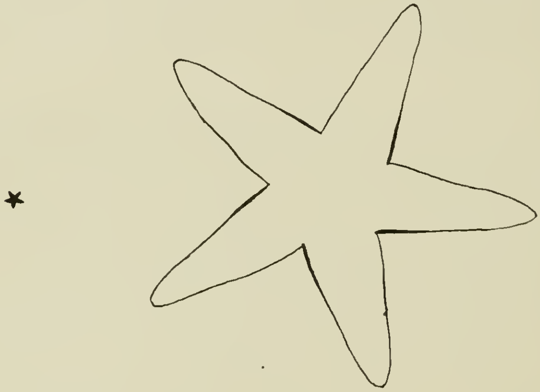


Fig. 2 *A*. Fig. 2 *B*.

These figures represent two starfishes of the same age (5½ weeks).

The age at which the starfish becomes sexually mature also depends upon the rate of growth; in other words, a starfish must attain a certain size before it may become sexually mature. During May, the month preceding the breeding season, nearly all the starfishes measuring over 50 mm. (2 inches) are full of ripe sex products, and occasionally ripe specimens are taken which measure only 32 mm. Larvæ have been obtained by artificial fertilization from parents measuring 38 mm. Now many of the starfishes raised in the car were considerably more than 38 mm. in length on October 25, three months after setting, and their sex glands were quite as well developed as they were in the average stars of any size at that season of the year. Allowing the very moderate estimate of 15 mm. for the growth of such individuals during the next six months, in May they would be more than 50 mm. in length, and such specimens are, with rare exceptions, sexually mature. We are warranted in inferring, therefore, that well-nourished starfishes arrive at sexual maturity and breed before they are a year old.

On the other hand, it is evident that many starfishes do not reach sexual maturity in one year, since small, immature specimens, between 10 and 20 mm. in length, are not uncommon just before the breeding season begins.

Desultory observations on other marine invertebrates, *e.g.*, the clam, oyster, and lobster, indicate that the conditions of their growth are essentially similar to those of the starfish, and to this extent substantiate the conclusion that between the higher and lower animals there are fundamental differences in the phenomena of growth.

BROWN UNIVERSITY,
November 9, 1899.

THE NATURAL HISTORY OF THE STARFISH.

By A. D. MEAD.

U. S. Fish Commission Bulletin for 1899.

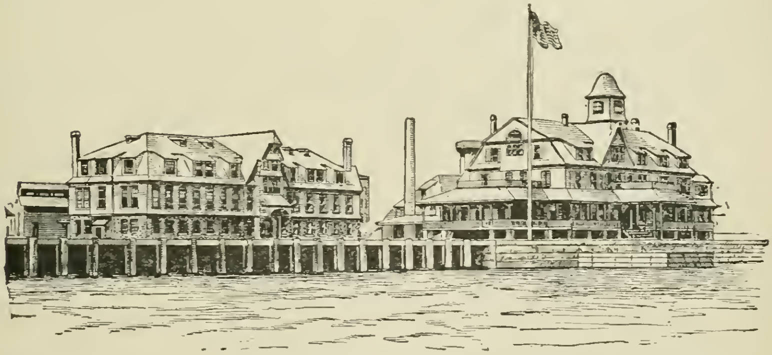
U. S. COMMISSION OF FISH AND FISHERIES,
GEORGE M. BOWERS, Commissioner.

CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION, WOODS HOLE, MASSACHUSETTS.

THE NATURAL HISTORY OF THE STAR-FISH.

BY

A. D. MEAD, Ph. D.,
Associate Professor of Comparative Anatomy, Brown University.



Extracted from U. S. Fish Commission Bulletin for 1899. Pages 203 to 224. Plates 23 to 26.

WASHINGTON:
GOVERNMENT PRINTING OFFICE.
1900.

Contributions from the Biological Laboratory of the U. S. Fish Commission,
Woods Hole, Massachusetts.

THE NATURAL HISTORY OF THE STAR-FISH.

By A. D. MEAD, Ph. D.,
Associate Professor of Comparative Anatomy, Brown University.

The investigation of the habits and life-history of the star-fish has been carried on at the suggestion and under the auspices of the Rhode Island Commission of Inland Fisheries. The observations were made principally at the Kickemuit River, Rhode Island, where a houseboat, moored over one of the oyster-beds, served as a floating laboratory. Through the courtesy of the U. S. Fish Commission in extending to me the privileges of the Woods Hole Station and in giving me the use of one of the steam launches I was able to make observations upon the star-fish in other portions of Narragansett Bay and to extend the work into Buzzards Bay. From oystermen I have received valuable information and assistance. and on every occasion the kindest treatment. The report is presented in the form of questions and answers, the questions being such as would be propounded by a practical oysterman, and intended to bring out information of value in combating the ravages of the star-fish. This paper, in slightly different form, appears in the twenty-ninth annual report of the Commissioners of Inland Fisheries for the State of Rhode Island, January, 1899.

IDENTIFICATION AND DISTRIBUTION OF THE STAR-FISH.

I. *Does the animal known to our fishermen as the star-fish or five-finger belong to one or to several species?*

It is evident that if there are two or more species artificial or natural agents destructive to one may prove quite harmless to the others. There are in Narragansett Bay 4 species of star-fishes, out of the 800 or more which are known to occur the world over. They are: The common star-fish (*Asterias forbesii*); the purple star-fish (*Asterias vulgaris*); the blood star-fish (*Cribrella sanguinolenta*); the snake star-fish (*Ophiopholis aculeata*). Only the first two species are considered in this report. The last two are so distinctly different from each other and from the first two that there is no difficulty in identifying them; neither is harmful to the shell-fish fisheries.

The common star-fish and the related purple star vary so much with regard to color, shape of arms, size, number of species, etc., that the French naturalist Perrier has made five distinct species of *Asterias* to include those star-fish along our coast which according to American naturalists, L. Agassiz, Stimpson, and Verrill, belong to two species only. I have endeavored during the last year to ascertain whether some of these varieties were to be explained as a difference in sex, but have been unable to discover any such relation, and am not able to distinguish males from females except by the sexual products.

II. *What is the geographical and bathymetrical distribution?*

The reply to this question will indicate the area subject or most liable to invasion. The purple star ranges from Labrador (probably farther north) to Cape Hatteras, and is most common north of Cape Cod. The common star ranges from Maine to the Gulf of Mexico, and is the species most common south of Cape Cod. The bathymetrical distribution of the purple star is from high water to 208 fathoms, and of the common star from high water to 20 fathoms.

From the numerous dredging expeditions of the U. S. Fish Commission launches and the steamer *Fish Hawk* carried on in 1898 it appears that in Narragansett Bay the purple star-fish (*Asterias vulgaris*) is practically restricted to the lower portion of the bay, below Gould Island, though occasionally, perhaps, taken farther north. One, for instance, was taken near Dyer Island, among 1,000 or more of the common species. I have never known a single one among the thousands of bushels of star-fish captured on the oyster-beds in the upper half of the bay. The common star, on the other hand, occurs in greater or less abundance everywhere from Fox Point to the mouth of the bay, and is the only species that commits depredations upon our oyster-beds. (The purple star would doubtless be destructive if it were present.) The stars from the vicinity of the oyster-grounds are, moreover, very similar to one another in appearance, as compared with those collected in one locality at Woods Hole, where one haul of the mops may bring up stars which apparently belong to several quite different varieties.

There are other varieties differing from those on our oyster-beds and from the purple star, which seem to be characteristic of certain localities. Thus, at the head of Buzzards Bay, at Neys Neck, a large number of common stars were collected, which were very similar to one another, but quite different from those on our oyster-grounds. They had very large coarse spines and were of a bronze color. The specimens taken by the *Fish Hawk* in waters south of Narragansett Bay seem to constitute a variety (maroon star) which occupies this area to the exclusion of other kinds.

It is not known certainly whether each of these so-called varieties is an actual variety in the sense that the individuals breed true, or whether the peculiar appearance is due merely to the fact that the individual stars are bred and reared in a particular locality. If it should prove to be true that the young of a certain variety, e. g., the maroon star, are always like the parent stars, no matter where they grow, we might be able to determine to what extent the star-fish are dispersed while in the free-swimming larval condition.

MODE OF LIFE.

III. *What is the method of locomotion?* (*It is possible that some barrier might be arranged that would limit, if not prevent, invasion.*)

The star-fish crawls or glides over submerged surfaces by means of the very numerous "suckers," or feet, which protrude from the furrows on the under side of the arms. Small stars, ½ inch or less from tip to tip, are frequently seen, ventral side uppermost, moving along with their suckers reaching up to the surface of the water. This performance can be carried on only when the water is very quiet, and is not often observed outside the aquarium. The buoyancy of the water and the great number of sucking feet enable the animal to crawl over the softest silt and the smoothest hard surfaces with ease, while the remarkable suppleness of the body enables it to get through incredibly small crevices. Besides this ordinary mode of locomotion, another peculiar method has been accredited to the star-fish by many, namely, that of clinging together in great clusters and rolling along the bottom with the tide.

The tradition is that large numbers of stars cling together to form a compact ball from 1 to 3 feet or more in diameter, which is rolled along the bottom by the tide until, striking an oyster-bed, the ball goes to pieces and the stars begin work at once. It is difficult to find an actual eye-witness of this phenomenon, though Ernest Ingersoll tells of an old oysterman, "Captain Eaton, of New Haven, who said that he and his brother once raked up the end of a cylindrical roll of star-fishes clinging tightly together, which they hauled into their boat until it would contain no more, when they had to break the roll or 'string,' as he called it, which was a foot or more in diameter." The "string" was composed only of star-fishes. I have never observed anything to confirm in the slightest degree the truth of these stories, though I have seen balls of star-fish clinging to each other. Upon examination it was evident that the stars were all endeavoring to devour some animal held in their midst.

For the purpose of testing the ability of star-fish to creep over soft surfaces, vaseline was smeared thickly on a vertical glass plate and on the under side of a horizontal glass plate. These plates were submerged in the aquarium with the star-fish, which measured 2 or 3 inches from tip to tip. The animals were observed to crawl over both these surfaces with no apparent difficulty. Paraffin was used in the same way and with the same result. It would appear, therefore, that submerged surfaces, though ever so soft or slippery, would not be effective barriers against the invasion of stars. They will not crawl out of the water, nor even protrude an arm above the surface, but will move along over a surface covered with a very thin layer of water, even if it is not deep enough to cover the whole body. They are perfectly secure, therefore, in a dish of water as shallow as a soup plate, so long as the water does not flow over the edge; but if placed in an aquarium which is constantly overflowing, they will frequently crawl over the edge and down the outside. No barrier, therefore, over which even a thin layer of water is flowing would be effective.

IV. *To or from what distance may star-fish migrate?*

This is a problem which has a decidedly practical bearing, but we have as yet very little accurate data for its solution. I have been told by several oystermen that stars sometimes suddenly appear in great numbers upon oyster-beds, and move over them at the rate of $\frac{1}{4}$ mile per day, more or less. It is generally understood, also, that there is some sort of a seasonal migration, especially noticeable in spring and fall, but the character and extent of this migration, if it really occurs, is unknown.

If a star crawled constantly in one direction at the rate of 6 inches per minute, which is a fair rate for a medium-sized one, it would travel about 4 miles in a month. At this rate star-fish could go from one end of the bay to the other in the course of the summer. But there is no good evidence that they take such extended excursions. The fact that they can be found all the year round in the upper part of the bay, and on the oyster-beds, shows that there is no wholesale migration to great distances.

There are some other facts which seem to indicate that the wanderings of these animals are rather limited in extent. Certain kinds of star-fish which are common in one part of the bay are not found, or are rare, in other parts. The purple star and "maroon star" do not migrate into the upper half of the bay, although the purple star, at least, might live in these waters, as I have found by keeping them in confinement. The star-fish in two neighboring parts of the bay, namely, Mount Hope Bay and Kickemuit River, do not seem to migrate back and forth, for those caught in Kickemuit River, during the past two years at least, were for the most part small, rarely measuring more than 3 inches from center of disk to tip of arm, yet about a mile from the mouth of this river there have been great quantities of very large stars with arms 4 inches long or more. In Barrington River there seems to be a great preponderance of small stars, about 2½ inches (arm) or less, of a reddish-brown color and thus distinguishable from the average star-fish caught in the vicinity of Nayatt. After the great freshet in the spring of 1888 nearly all of the star-fish in the Kickemuit River perished, Mr. Bourne tells me, and were not again troublesome for three or four years.

These facts, though not conclusive, lead to the conjecture that natural barriers to the migrations of star-fishes exist in our bay. Some of these may be, depth of water, density of water, or a strip of barren bottom. If the conjecture is correct, that the migrations of the star-fish are confined to comparatively limited areas, the prospect of diminishing their numbers by a systematized effort is encouraging.

V. *What animals are devoured by the star-fish for food? If the young star-fish feed habitually upon certain animals, it is possible that the destruction of the latter will cause the former to perish.*

Star-fish, especially when young, are exceedingly voracious feeders, prey upon oysters, clams, mussels, barnacles, various kinds of sea-snails (including oyster-drills), worms, and small crustacea, and, if slightly pressed by hunger, turn cannibals and prey upon smaller star-fish. From its depredations upon the oyster-beds of New England the star-fish has become notorious. Collins (Notes on Oyster Fishery of Connecticut) estimates that in 1888 the damage done to the beds in the Connecticut waters alone was $631,500, although 42,000 bushels of stars were taken from the beds that year.

It was found during the summer of 1898 that the star-fish in Mount Hope Bay and in the vicinity of Nayatt were feeding in great numbers upon a little bivalve which closely resembles a young quahog, but which is an adult mollusk of another species (*Mulinia lateralis*). Fig. 1 represents a large specimen, natural size. The *Fish Hawk* recently found these animals exceedingly abundant in certain parts of the bay.

Mussels are a favorite food of the stars, and doubtless many thousand bushels of mussels are devoured by them every season. Indeed, some of the mussel beds have disappeared within the last few years, having been destroyed, probably, by the stars. Unlike the oyster-beds, the mussel-beds are not protected from the onslaughts of the stars, and we can appreciate the extent of the damage to the mussel, if we imagine the condition of a bed of small oysters unprotected from star-fish for a single season.

In rearing the young stars for the purpose of studying their rate of growth, etc., I found them to be very fond of small clams and barnacles, as well as of young oysters. A more detailed reference to the damage done to young clams by the star-fish will be found on p. 215. I have caught stars in the act of devouring oyster-drills, and believe it probable, therefore, that the drills, which are a serious menace to the oysters in some localities where the star-fish are rare, are to some extent held in check by the stars.

VI. *What is the method of feeding?*

The mouth of the star fish is in the center of the disk on the lower side of the body. Comparatively small pieces of food are taken into the stomach, and the refuse ejected again through the mouth. But, since the mouth is small (about ¼ inch in a good-sized star) and surrounded by calcareous plates, larger animals, which form the greater part of the star-fish bill of fare, are necessarily digested without being taken in through the mouth. The stomach therefore is turned inside out and, wrapping itself about the animal to be devoured, digests it where it lies, and is then withdrawn to its normal position within the body. It is safe to say that the stomach can be protruded for a distance equal to the length of the star-fish's arm.

The greater part of the animals upon which the star-fish prey are mollusks protected by hard shells; for example, the sea-snails, mussels, quahogs, and oysters. How does the star get at the soft part of the mollusks? This question has given rise to a great deal of interesting, not to say amusing, speculation, especially with respect to the oyster. An old tradition in England and this country is to the effect that the star takes the oyster by suprise and puts an arm into its gaping shell; then a fight ensues. Sometimes the oyster is victorious, while the star-fish retreats minus an arm, but often the oyster succumbs, since it can not live long with its shell open, and the star then devours its prey at leisure. There are two facts that are sufficient to disprove this theory. In the first place, the oyster is very sensitive and feels the slightest disturbance in the vicinity of the margin of the open shell. In the second place, the shell does not open wide enough to admit the arm of the star. Moreover, simple observation of the star-fish during the process of eating disproves the story.

It is supposed by many that the star-fish injects a poison into the shell which causes the latter to open. But the valves of the shell can be shut water-tight and would exclude such a poison. I have taken away from the star-fish oysters, mussels, and drills which had already been opened, and placed them in an aquarium, where they soon recovered and behaved as though nothing had happened. Schiemenz found the same to be true in the case of the quahog (*Venus*).

Some have supposed that the star bores a hole through the shell of the victim, but the star has no boring apparatus, and the shells known to be opened by the star have no holes in them.

It is a very common belief that an acid is secreted by the star, which dissolves the shell so that an entrance is effected. After a successful opening, however, the litmus paper shows no acid from the stomach of the star-fish, and the margin of the shells shows no trace of having been acted upon by an acid. A considerable quantity of acid would be required to sufficiently dissolve the shell of a medium-sized oyster, and this would undoubtedly dissolve, at the same time, the unprotected calcareous spines about the mouth of the star-fish itself.

The most prevalent opinion is, perhaps, that the star chips away the thin edges of the shell until an entrance is gained to the soft parts. The broken edges of oyster shells which have been opened by the star seem at first to sustain this opinion. The process is thus described in a Providence newspaper:

> The star-fish seizes its prey by clasping its tentacles around the soft, fringy edge of the oyster, which it eats away until the soft oyster can be sucked from the orifice, etc.

Ingersoll, in an article on the oyster industry, after speaking of the alleged use of acid in opening the shell, says:

> Moreover, it seems unnecessary, since the appearance of every shell attacked at once suggests the breaking-down, chipping-off movement, which the star-fish might easily produce by seizing and suddenly pulling down with the suckers nearest the mouth, or by a contraction of the elastic opening of the stomach. At any rate, the thin edge of the shell is broken away until an entrance is made which the oyster has no way of barricading.

An oyster which has not been injured by rough treatment has the edges of the shell extremely thin and so fragile that they can be broken down with a camel's hair brush. The lower shell is particularly fragile near the edge. It will be noticed, however, that the valves frequently do not come together at all at the extreme edge, and the real line of contact, the biting edge, is one-fourth inch or more further back. The chipping of the margin of the shell by the star-fish is merely accidental, and avails nothing in getting at the soft parts of the oyster. I have carefully examined a large number of shells of oysters known to have been devoured by star-fish, and, though they appear to be badly chipped, the biting edge is never broken, and the shells have always been found to be water tight. If such a shell, recently opened by the star, be filled with water, and the valves held between the thumb and the finger, the water will not leak out even though the shell be violently shaken.

In mussels which have been opened by the star-fish there is no trace of any chipping at all. The reason is plain: the valves of the shell come together firmly at the very edge; there is no delicate fringe at the margin. The same is, of course, true of the quahog. Nevertheless, the small quahog and mussel are readily opened by the star-fish. It follows, therefore, that if the star gains entrance to the soft oyster by chipping off the edge of the shell, a different process must be adopted in entering a mussel or quahog, to say nothing of the snails which it also devours.

The credit of solving the problem—How do the star-fish open oysters?—is due to Dr. Paulus Schiemenz of Hanover, Germany, who carried on his investigations at the famous zoological station at Naples. The problem was suggested to him by Collins's report of the enormous injury done to the oyster-beds by the star fish in Long Island Sound. The process is briefly as follows: The star-fish so covers his victim that the suckers on the under side of the arms are distributed, part to one valve, part to the other, and the remainder frequently to some surrounding object. (In the case of the snails the suckers are attached to the operculum and to the shell.) The suckers are very numerous and stick fast, and a tendency to straighten the arms results in a constant pull on the shells in opposite directions, which, if strong enough, would open the shells. It is true that a star-fish is not strong enough to open an oyster or quahog immediately in this manner, but it can and does fatigue its prey. The constant, steady pull in opposite directions soon fatigues the muscle which holds the shell together, and the oyster or clam presently gapes open. The oyster can overcome a strong pull for a short time, but not a weaker pull for a long time. The same principle is well illustrated in the case of the periwinkle or conch. If a string be tied around the "foot" so as to give a good hold on the animal, a strong man can not pull the mollusk out of its shell, but if it be suspended by this string it can not sustain for a long time even its own weight. On the same principle a man who can hold at arm's length a weight of 20 pounds can not hold his empty hand in this position for 10 minutes. Schiemenz showed by experiment that the star-fish could exert a pull of over 1,200 grams, and that a pull of 900 grams is sufficient for opening a good-sized quahog if allowed to act for 30 minutes.

Often more than one star takes part in opening an oyster, and when opened other stars often enter into the feast. It is the young oysters that are in greatest danger from the stars, and the danger decreases as the oysters grow larger. Oysters of marketable size, that is, three or four years old, are comparatively unmolested. Of course the larger stars can open the larger oysters, but fortunately the larger ones are more easily caught in the "mops" and thus more easily kept off the beds. It has not been ascertained how large an oyster can be opened by a star-fish.

VII. *At what season of the year do the star-fish spawn? If at a particular season, a special effort should be made to kill the animals before spawning, and thus destroy both stars and spawn.*

I have attempted by two methods to determine the spawning season of the star-fishes in the upper portion of Narragansett Bay and at Woods Hole. The first method consisted in examining a large number of adult stars at intervals during the year, to see if they contained ripe eggs and milt. The second method consisted in dragging a fine silk "tow net" at the surface of the water, to catch the free-swimming young.

Most of the adult star-fishes examined were obtained through the kindness of the oystermen in Kickemuit River, Mount Hope Bay, and the vicinity of Rocky Point. On July 19 and 22, 1897, 630 stars were carefully examined, and the sizes of specimens and of sexual glands were tabulated. The specimens ranged from 1¼ to 3½ inches (taking distance from mouth to tip of arm). Fifteen contained eggs or sperm apparently ripe. In some, only one arm contained ripe products. None of these apparently ripe specimens were smaller than 2 inches. In the great majority the sexual glands were small, less than one-half the length of the arm. During the remainder of the summer, stars from these localities were frequently examined, and occasionally one was found with ripe eggs, but there was no general increase in the size of the glands.

On November 15 a lot of stars from Rocky Point was examined. They were nearly uniform in size, and measured about 3 inches. In about half of these specimens the glands were half the length of the arm, but none were ripe. Among the 75 specimens, measuring approximately 3 inches, collected at the same place November 29, 14 seemed to be nearly mature; the glands in 44 others were half the length of the arm; the remainder had small and immature glands.

January 6, 1898, Rocky Point: About 40 stars, 3½ to 4 inches in length, were examined. Only 4 had sexual products which seemed to be nearly ripe, while the majority seemed less mature than in November.

January 7, Kickemuit River: 50 stars ranging between 2½ and 3½ inches (4 specimens measured 4 inches). In 20 specimens the glands were considerably developed, but not nearly ripe. In the remaining 30 they were quite small.

January 15, Kickemuit River: 50 stars, measuring from 2½ to 3½ inches were examined. In general, there was, perhaps, a slight increase in size of glands, though in over 30 they were very small.

February 9, Rocky Point: 126 stars, 2½ to 4 inches long. In 3 the sexual products were ripe; in 10, nearly ripe; in 53, large and turning color, becoming slightly pink; in 47, small, but showing signs of seasonal development; in 12, very small.

February 12, Kickemuit River: 63 specimens, measuring from 2 to 3½ inches. In 6 the glands were large and beginning to show a pink color; 39 showed seasonal development, while 18 were very small.

March 4, Kickemuit River and Mount Hope Bay: 39 specimens, 2½ to 3½ inches in length; 1 was apparently quite ripe; 26 seemed nearly ripe; the glands in 7 were beginning to change color; in 3 immature but showing seasonal development; in only 2 specimens were the glands very small.

March 7, Rocky Point: 99 specimens, measuring 2 to 3½ inches; 5 were apparently fully ripe; 71 nearly ripe (very large glands); in 20 the glands showed the pink color slightly; in 2 the glands were small, but showed seasonal development; only 1 had very small glands.

It is evident that, during the latter part of January and throughout the month of February, there is a regular increase in the size of the sexual glands in nearly all the star-fishes from Rocky Point, Mount Hope Bay, and Kickemuit River. By the end of the first week in March, the great majority appear to be nearly mature, while the others, except in a few cases, show a distinct seasonal growth in the sexual glands. The stars at this time begin to look "fat," because of the increased size of these glands and of the digestive glands, usually called the "liver," which fill the arms.

April 5, Rocky Point: 197 specimens examined, varying in length from 2 to 4 inches; 137 had the appearance of being fully ripe; 32 were nearly ripe; in 20 the glands were beginning to show the pink color; in 9 they were smaller, but showed seasonal development; in 1 only were the glands very small.

April 13: 25 specimens, out of a basketful from Mount Hope Bay, were examined. All seemed ripe, and so the examination was not carried further. Although during the first two weeks in April the stars are all *apparently* ripe, they do not discharge the products for about two months. During this time they appear to be extremely "fat."

On May 17 the stars were examined again in Kickemuit River and Mount Hope Bay, and appeared very much as in April. They were, perhaps, more distended with spawn and milt, but had not yet discharged.

During the first four days of June, star-fish from many localities in the upper portion of the bay were examined on board the launch *Sagitta*, engaged by the United States Fish Commission. The stars were, almost without exception, full of very ripe eggs and sperm, which were easily shaken loose in the water. Small specimens, measuring in many instances only 1¼ inches, were fully ripe.*

The height of the spawning season occurred between this date, June 4, and June 16. From June 16 to June 28 the star-fish examined in many localities, especially at Kickemuit and Rocky Point, had extruded most of their eggs or sperm, but in some the ripe spawn was found in one of the arms, or merely in the base of the arms, as though not quite all had been extruded. Specimens in which some ripe products were left were more frequent on the 16th than on the 21st, 22d, and 28th of the month, which indicates that the spawning season was rapidly drawing to a close.

Star-fish examined in July, and occasionally during the rest of the summer, yielded the same results as those examined at the same season in 1897; most of them had very small sexual glands, but some were found with products apparently ripe.

On June 22 I searched carefully on the seaweed and eelgrass in Kickemuit River for very young stars, but not a single one (under one-half inch or more) could be found. On June 29 another careful search was made in the same locality, and countless numbers of minute stars were found, most of them about the size of the head of a pin. They were clinging by dozens to every spear of eelgrass, and scattered diffusely through the branches of fluffy seaweed, which is abundant in this locality; the larger of them were probably not more than a few days old (since time of setting), as I afterwards determined by watching the growth of those whose exact time of setting was known. Doubtless, therefore, the small stars were absent, and not overlooked, in the search on June 22. I feel sure, therefore, that in this locality the star-fish first begin to set, in considerable numbers, on June 28, or within a day or two of that date.

The first attempt to capture stars in the free-swimming stage of their existence was on June 27, at Kickemuit. The tow-net was dragged at the surface at intervals for two hours in the evening. The weather conditions were unfavorable, as I afterwards learned, and for this reason no young stars were caught. On the following morning, June 28, a great many fry were swimming at the surface of the water. From this date until July 16 they could be taken at any time, unless conditions were particularly unfavorable. The few larvæ caught on July 16, however, were old, and all of them set in the aquarium during the next 12 hours. After this no more larvæ could be obtained. though the next few days were exceptionally favorable.

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* See remarks on "Age and size at sexual maturity."

It is evident, therefore, that in Kickemuit River the season during which the star-fish larvæ set in considerable numbers began about June 28 and ended about July 16, a period of a little less than three weeks. Allowing that the larvæ set three weeks after the spawn is laid (which is the period given by Ingersoll), we may conclude that the beginning of the spawning season was about June 7, and the end June 28, while the height of the season was the first, and possibly the second, week in June. From the observations of the sexual glands of the adults, it appeared that the greater part of the spawn was extruded between the 4th and 16th of June. The facts, therefore, obtained by both of these methods agree very closely.

From Dr. Seitaro Goto, of Tokyo, Japan, who worked in Mr. Agassiz's laboratory at Newport in 1895, I have obtained the following interesting data. For one or two days before July 15 the larvæ had been very numerous. On the 15th they were decreasing in number, and after July 20 none were found. At Newport in 1895, therefore, the breeding season was nearly the same as that at the Kickemuit River in 1898.

At any time in the year a few star-fishes may be found which contain ripe eggs and spermatozoa, but it is not known that these eggs are laid out of season. If they are, the chance of their becoming fertilized is small. Dr. Goto writes me that a similar phenomenon is seen in a Japanese species of sea-urchin. He is able to obtain ripe eggs and sperm, and to fertilize the eggs artificially, even in the midst of winter, though the species probably does not breed in these waters at that season.

To answer briefly the ninth question we may say: The stars in the upper part of Narragansett Bay, and probably throughout the bay, have a short spawning season, beginning about the second week in June and continuing two or three weeks. The young fry begin to set the last week in June and continue to set until the middle of July. The fact that ripe stars may be obtained in very small numbers throughout the year is of no practical significance, for if they lay their eggs out of season the chances are comparatively slight of their being fertilized.

Observations were made at Woods Hole from March to the end of the summer I is rather difficult to interpret the results satisfactorily, for at no one period were more than a small proportion of the stars at Woods Hole ripe, or even approaching a ripe condition, and, on the other hand, a few ripe specimens could be found at any time. As a rule the sexual glands were very small, like those of the Narragansett Bay stars in midwinter, and it was noticeable also that in such specimens the digestive glands were also unusually small. The latter condition I take to be an indication of poor nourishment, judging from the condition of poorly fed stars kept in confinement as compared with well-nourished specimens. I am inclined, therefore, to assign the failure to breed to the same cause.

In this connection I may observe that in the specimens kept over winter at Kickemuit, with very little to eat, the sexual glands did not approach a ripe condition. An examination of stars taken in February and March from Narragansett Bay shows that by this season of the year they are eating voraciously, shells and even fragments of star-fish being found in their stomachs. In some years the stars have bred in abundance at Woods Hole, but the notes on the time of breeding are somewhat puzzling, as they indicate that the time varies considerably.

VIII. *What are the habits of the "fry" or free-swimming young? The young of many marine animals, while far more abundant than the adults, are much more delicate and easier of extermination.*

The ripe eggs of the star-fish are minute spherical objects, measuring about one-tenth the diameter of the head of a small pin. They are discharged from the female through minute pores near the base of each arm, into the water, where they may become fertilized by the spermatozoa discharged from the male in a similar manner. Each egg, soon after it is fertilized, begins to undergo a long series of changes in form. During the first stages of development there is little or no increase in size, and the egg rests, like a minute grain of sand, upon the bottom. In the course of a few hours, however, the internal changes which have been taking place express themselves. Vibratile cilia appear in certain areas on the surface of the egg, which now begins to rotate, and soon rises from the bottom as a free-swimming larva. Soon after this the mouth and stomach are developed, and the creature takes in food and grows. The growth is rapid, and during the next three weeks, more or less, the larva increases its diameter about 50 times. Meanwhile various internal organs and several long arms, and other external features, are developed. The older fry are called brachiolaria, from the fact that they have so many long arms. One of these brachiolaria of the largest size is represented in fig. 3, much magnified. The natural size is shown in fig. 4. where two specimens are figured, one on either side of the bit of eelgrass. The animal swims by means of the motile cilia, which are arranged in bands, represented by the heavy lines in the figure. They form a complicated pattern over the surface of the body, and extend out upon the arms. The body is quite transparent, and the tips of the arms, which are shaded in the figure, are light red. The larva represented in fig. 3 is old, and would probably have set within 12 hours. Already the rudiment of the resulting star-fish, the disk-shaped body at the bottom of the figure, can be seen within the brachiolarian. The five crenate lobes on the margin of the disk are the beginning of the five arms. The disk itself at this time is already somewhat opaque.

When the larva is about to "set," it attaches itself to some object, like a spear of eelgrass, by the suckers, shown at the top of the figure, and then a rapid transformation occurs. The whole superstructure above the disk collapses and becomes absorbed like the tail of a tadpole. In a few hours the brachiolarian has disappeared, and a star-fish proper has taken its place.

Although the free-swimming larvæ have a considerable power of locomotion, and can swim from one side of a dish to the other in a few minutes, they can not, of course, make headway against the tidal currents, and are carried hither and thither with their ebb and flow. Other extensive movements of larvæ are executed in response to such changing conditions as those of light and temperature; at times myriads of them are swimming at the surface, and in 12 hours not one specimen can be found. The brachiolarian, like more lowly organized forms of living creatures, although it has no eyes, is exceedingly sensitive to light, sometimes being attracted to it, and again being repelled by it. According to my experience, they were found at the surface in greatest abundance on cloudy or misty days and nights, and were much more rare, or absent altogether, on bright, clear days and moonlight nights. On June 27, for instance, I skimmed the surface with the tow-net from 9 until 11 o'clock, and not a single larval star was found, although there were millions of the larvæ of the annelid worm *Syllis*, and other organisms. The night was clear, with a bright moon, and the tide was rising. The next morning, June 28, was cloudy with some rain, and large numbers of the larvæ were taken in the nets, between 8.30 and 10 o'clock. In the evening of this day, between 9 and 11 o'clock, they were even more abundant than during the day. The evening was calm and cloudy, with a little rain. Afterwards I met with the same experience on several occasions.

Another question in respect to the movements of the free-swimming larvæ is of practical importance, inasmuch as they are thousands of times more numerous than the adult stars. To what distances may the larvæ be carried by the tides and currents in our bay? I can not answer this question directly, but there are certain facts which have an important bearing upon it.

Although the purple stars (*Asterias vulgaris*) are common in the lower portion of the bay in the vicinity of Newport and Seaconnet, they seem to be totally absent from the upper parts, although the adults, at least, can live in these waters. I have kept them for a long time in Kickemuit River. This would seem to indicate that the larvæ of purple stars are not transported by the tides from the lower to the upper portion of the bay. It may be, of course, that the larvæ, unlike the adults, can not abide in the upper portion, or that the young stars, as soon as they can crawl, return to the southward unnoticed; this seems to me, however, to be improbable.

The distribution of some other marine animals whose habits are similar to those of the brachiolaria is of interest in this connection. At Waquoit, about 10 miles northeast of Woods Hole, on the Vineyard Sound side, the water was fairly alive with the young of a certain species of jelly-fish, which could be obtained from this locality in immense numbers at any time for several weeks during the spring. At Woods Hole, however, these specimens were comparatively rare. Again, later in the summer, at Menemsha Bight, near Gay Head, another small jelly-fish was found in such abundance that every bucketful of water contained thousands of specimens, yet they were exceedingly rare, if present at all, at Woods Hole.

In the upper part of Buzzards Bay, at Neys Neck, the star-fish probably bred in great numbers, judging from the appearance of the adults earlier in the spring, yet the larvæ were rarely caught at Woods Hole.

These facts, and others of the same nature, certainly suggest that the larval star-fish may not be transported to great distances in the bay by the tides.

IX. *What are the habits of the young star-fish? It is possible that the young star-fish, like the young of many fish, tend to gather in schools. If so, the young might be killed off in thousands.*

The data with reference to the habits of the young stars were collected at Kickemuit, where it was possible to have a certain area along the shore under constant observation. Up to the very time when the larvæ are ready to set they swim freely in the water; and larvæ, caught in the tow-net, often set in the dish of water before I had returned to the houseboat, i. e., within an hour of the time they were caught. In this condition they attach themselves by their suckers (see fig. 3) to any object they happen to strike, and cling to it with great tenacity until the metamorphosis is completed. As the larvæ are borne along by the currents, the eelgrass, rockweed, and especially the fluffy, branching seaweed, naturally catch immense numbers of them. I think it would not be an exaggeration to say that on a single handful of seaweed which I picked up about the 1st of July there were more than a thousand young stars. For the next three weeks they remain for the most part crawling about over this vegetation, gradually working down among the roots of the rockweed and upon the large stones at the bottom. They grow rapidly during this time, but decrease in numbers, for they are bright and conspicuous objects for the small fishes; yet they are exceedingly numerous for a long time. In order to obtain a definite expression of their abundance, I scooped up a large handful of the fluffy seaweed, which, together with the water, filled about two-thirds of a paper pail, and from this 603 young stars were taken. The average size was about that in fig. 9. A cart load of seaweed taken out at this time would have destroyed millions of star-fish.

By the 1st of August the fluffy, branching seaweed, which bore so many young stars, was nearly all dead, and though the stars were still present in great numbers upon the eelgrass, rockweed, and stones covered with sea-moss, they were also frequently seen crawling along the muddy bottom. By August 15 the eelgrass was overgrown and lodged by a luxuriant growth of *Botrylus*, a compound ascidian, which appears as dark gelatinous patches. The small stars were still numerous upon it, but were rather thin and poor. The larger and better nourished stars had left the eelgrass and were searching for food upon the stones and along the bottom.

The small star-fishes, such as live upon the eelgrass, are remarkably hardy in some respects. They will live for weeks, and even months, in a small dish, without change of water and with a minimum amount of food. During the first week in July I carried a number of free-swimming brachiolaria, like fig. 3, to Providence for further examination. They were in a glass 1-quart jar, and, after one or two were taken out, the jar was closed and was left unopened during the rest of the summer. In a few days the larvæ had all set, and when I examined the dish again, on September 5, it contained still a few live stars, which were, however, very small. Upon watching them it was seen that the more enterprising individuals were eating their companions, and finally only one remained. This one lived in the jar for weeks, but, unfortunately, I am not able to record the exact date of his death.

On the other hand, the same young star-fishes, which can live so long without food or change of water, perish quickly if left out of the water, especially if the sun is shining. They can not live, therefore, above the low-water mark, unless sheltered by a dense growth of vegetation. Large stars can endure very much longer exposure, since their bulk prevents their drying so quickly. On July 16 I made a special search for young stars on the sea-weed, above the low-water mark. I found none, yet just below low-water mark they were excessively abundant. At the same time it was noticed that above the line where the star-fish were abundant there was a thick set of 1-year old oysters, while below it the oysters were absent. The oysters set somewhat later in the season than the star-fish, and the latter, therefore, are ready to prey upon the young oysters as soon as they appear. When, in addition to these facts, we take into account the extraordinary voracity of the young star-fish, their immense numbers, and their special fondness for oysters, we are led to conclude that one reason why a considerable set of oysters is so rarely obtained below low water is that they fall prey to the star-fish. The oysters which set above high water are comparatively safe, for when the tide leaves them uncovered they can endure for hours the direct heat of the sun, which would kill the young star-fish in a few minutes.

While the star-fish are living upon the eelgrass and seaweed they are supplied with an abundance of food in the form of the young of marine worms, snails, and other animals, which, like the stars themselves, swim freely in the sea for a time, and then settle down upon any object with which they happen to come in contact. Throughout July the water at Kickemuit was teeming with minute free-swimming creatures, and in the aquarium the growth of the youngest stars could be greatly accelerated by feeding them the contents of the tow-net. During the last four days of June innumerable larvæ of a marine worm (*Syllis*) were swarming at the surface, and on July 11 millions of the young of one of the sea-snails (*Littorina?*) were caught in the tow-nets.

The clam, also, is one of those unfortunate animals whose larvæ set at about the same time as the star-fish, and in the same places. The star-fish before they are 3 days old show a predilection for young clams, which apparently does not diminish so long as any clams remain. Fig. 2 was drawn from life last summer by Dr. J. L. Kellogg, and represents a characteristic scene in the marine tragedy.

In order to ascertain how fast the stars of the average size found upon the eelgrass would devour the young clams of average size, I placed one such star in a dish with 56 clams taken at random from the margin of a stone. The larger clams were about the length of one arm of the star, and they ranged from this length to 1 or 2 mm. The experiment was begun at 1.22 p. m. on July 18; at 5.40 p. m. 2 clams had been devoured, each about the length of the arm of the star, and during the evening a third was eaten. At 8 o'clock the following morning 5 had been eaten, at 9 o'clock 6, and at 9.05 the seventh clam had been attacked. I was absent from the laboratory for the next 4 days, and, returning on the 22d, found at 6 p. m. 29 empty shells whose contents had been eaten by the star, which had grown considerably and was eating faster than formerly. The next day 39 empty shells were found, and on the following day 46 were empty, while 10 more had disappeared altogether, having doubtless been devoured, shell and all, some time during the week. To make sure that the clams were killed by the star and did not die from some other cause, a control dish of clams was kept, in which all the specimens lived. *In six days a single star-fish devoured over 50 clams.* Both star-fish and clams represented the average size at this season. I regret that I did not record the exact dimensions of the star at the beginning of the experiment. Fig. 11 shows its approximate size at the end of the experiment on July 25.

When we recall how exceedingly numerous star-fish are, and that they are found in the same localities with the young clams, the result of this experiment becomes still more significant. At this rate 600 stars from one netful of seaweed could devour 30,000 clams in 6 days. The star-fish in a cartload of seaweed, if it contained 200 small forkloads, would have the capacity for destroying over 6,000,000 clams in a week.

From the foregoing it appears that the star-fish set for the most part during the last few days in June and the first week in July, some as late as July 16. They remain upon the seaweed in immense numbers until about the 1st of August, when many of them are found upon the bottom. By August 15 the greater portion of the stars have left the seaweed and gone to the bottom. The young stars do very great damage, not only to the young oysters, but also to the young clams.

The stars could be destroyed by hundreds of thousands in July by collecting and drying a few cartloads of seaweed taken below low-water mark. After the first week or two of July the collection of seaweed would do no injury to the clams.

X. *What is the rate of growth up to sexual maturity?*

The observations and experiments bearing upon this question were made at the Kickemuit River, and these methods were adopted:

(*a*) A large number of star-fish were kept under constant observation and were surrounded with natural conditions as far as possible.

(*b*) Frequent observations were made on the stars in their natural environment.

(*c*) Individual star-fish were reared under various conditions, and their growth recorded from time to time.

(*d*) Star-fish which were regenerating lost parts were kept under various conditions, to determine the rate of growth and the rate of regeneration.

(*a* and *b*) On June 29 a bunch of seaweed, on which were hundreds of small stars, was placed in a car at the house-boat. All the stars were very small. The greater number were about the size of that in fig. 5, but they ranged from the size shown in fig. 4, just setting on the eelgrass, to that in fig. 6.

On July 15 it was found that hundreds of stars had crawled through the wire netting and were thickly scattered about on the under side of the car. Here they had found an abundance of small barnacles, which to all appearances they very much relished. After preserving a few specimens, to compare with those taken from the seaweed, the rest of the stars were left unmolested upon the bottom of the car. The average size of the stars on the car was greater than the average of the larger specimens on the seaweed. This was doubtless due to the fact that the former were better fed. A difference in shape was also striking, those on the car being more plump. Figs. 7, 8, and 9 represent three specimens taken from the seaweed on this date, and fig. 10 one of the larger specimens (3 mm. from mouth to tip of arm) from the car, all natural size. The measurements which follow are all taken from mouth to tip of arm.

On July 18 the stars showed a very appreciable growth. One of the larger specimens, measuring 5 mm., is represented natural size in fig. 11.

On July 24 one of the largest measured 8 mm., and was preserved (see fig. 12).

On July 26 one could see an appreciable growth since the 24th, and the specimen shown in fig. 13 measures 9 mm. In 11 days (since July 15), therefore, there has been an increase of 300 per cent in the length of the arm, which is equivalent to a much larger increase in bulk.

The stars were taken from the bottom and put inside the car on August 1 and were fed with barnacles and small mussels. They had by this time eaten nearly all the barnacles on the bottom of the car and were doubtless in want of food.

On August 2 the largest specimen measured 11 mm., and is represented in fig. 14. Those on the bottom, however, which had left the eelgrass, were larger, some of them approaching the size of those on the car.

On August 13 a box thickly covered with barnacles was split up and pieces put into the car. The star-fish always preferred the under side of the boards, and the latter were therefore placed barnacle side down.

The stars on the eelgrass were examined on August 15 and the larger ones averaged about 2½ mm., or about the size of that in fig. 9.

On August 18 the largest measured slightly less than 18 mm (see fig. 15). This specimen was afterwards kept in a dish without food, and will be referred to again.

On September 5 one of the largest specimens was 26 mm. in length of arm (fig. 16). Another measured 27 mm., and several measured 25 mm. or more.

On September 26 the largest measured 35 mm., and is represented in fig. 17.

On October 12 the largest found was 42 mm. (fig. 18).

On October 25 one specimen measured 54 mm., or about 2¼ inches (fig. 19); this was preserved. The next largest (51 mm.), shown in fig. 19, is the largest star reared in captivity. It was almost exactly 4 months old, having set about June 28. The sexual glands were more highly developed than usual, even for larger stars at this season. From this date to November 11 there was no growth, but apparently a slight decrease.

The following gives in brief the measurements of some of the largest stars found on the car during summer and fall. The asterisk (*) indicates that the specimen was not returned to the car, so that a smaller specimen was recorded on the next date.

Date.	Millimeters.	Date.	Millimeters.	Date.	Millimeters.	Date.	Millimeters.	Date.	Millimeters.
July 15	3	Sept. 5	25	Sept. 26	34	Oct. 12	38	Oct. 25	45
July 18	5*	Sept. 5	25	Sept. 26	33	Oct. 12	36	Oct. 25	44
July 24	8*	Sept. 5	25	Sept. 26	33	Oct. 12	35	Nov. 5	45
July 26	9	Sept. 5	24	Sept. 26	31	Oct. 12	35	Nov. 5	44
Aug. 2	11	Sept. 5	24	Sept. 26	30	Oct. 25	54*	Nov. 5	43
Aug. 18	18	Sept. 5	24	Sept. 26	30	Oct. 25	51	Nov. 5	43
Sept. 5	27	Sept. 5	23	Oct. 12	42	Oct. 25	50	Nov. 5	43
Sept. 5	26	Sept. 26	35	Oct. 12	40	Oct. 25	48	Nov. 5	42
Sept. 5	26	Sept. 26	35	Oct. 12	40	Oct. 25	45	Nov. 5	40

On September 5 a number of specimens (19 in all) were selected and placed by themselves in another car, so that I might be sure to measure the same individuals on succeeding days; these were measured on six occasions, with the following results:

Specimen.	Sept. 5.	Sept. 26.	Oct. 12.	Oct. 25.	Nov. 5.	Nov. 11.
No. 1	24	35	40	47	46	41(?)
2	24	31	35	40	38	41
3	20	30	35	38	38	40
4	19	29	34	38	38	39
5	19	29	33	38	38	38
6	19	28	32	37	38	38
7	18	28	32	36	38	36
8	18	28	31	36	37	36
9	18	27	31	36	37	35
10	18	26	30	36	37	35
11	17	26	30	35	37	35
12	16	26	30	35	37	35
13	16	25	29	35	34	35
14	16	25	29	35	35	35
15	15	24	28	34	33	34
16	15	23	28	32	33	34
17	15	21	27	30	32	33
18	14	21	25	30	32	31
19	12	21	....	29	31	31

It will be noticed that among these specimens, as well as among those in the original car, given in the first table, there is rarely any evidence of growth after October 25, but there is rather a slight decrease in size. On each occasion the measurements were made without referring to those of the preceding date, so that no personal prejudice might enter the results. For the most part the figures indicate a fairly uniform rate of growth among the different stars. In interpreting these figures there is one factor which is to be taken into consideration, namely, that star-fish over 20 mm. (sometimes less) are able to contract and expand, so that two careful measurements, taken within a few minutes of each other, may vary as much as 1 or 2 mm. The measurements in the last three columns, therefore, indicate that the star-fish in the car were of about the same size on November 11 as on October 25. The first measurement (41 mm.) under November 11 is doubtless an error.

It may be inferred, from what has already been said, that at any time during the summer, after the stars are all set, there is a great difference in size among them. To illustrate this point, I arranged on August 18 a series of specimens taken from the car and from the seaweed, and photographed them at natural size, by laying them down on the sensitive paper (with a thin transparent film between), and then exposing. The variation in size is shown in fig. 20, the first 5 specimens having been taken from the car, and the last 5 from the seaweed. This variation in size is doubtless due much more to the difference in amount of food than to difference in age.

The following experiments on the rate of growth support this view:

(*c*) *Rate of growth of individual star-fishes kept under various conditions.*—The largest of the stars in the car on August 18 (compare fig. 15) was kept in a dish with only a few very small barnacles for food. When taken from the car, it measured 18 mm.: slightly more when fully expanded. On September 25 it measured 18 mm., showing no growth. On September 26, 39 days after it was taken from the car, it measured between 15 and 16 mm. In the absence of food, therefore, it had lived and apparently was in perfect health, but had probably diminished somewhat in length, as well as in bulk. (Some allowance must, of course, be made for the contraction and expansion, as mentioned before.) During this time several of the stars, smaller than this one, remained in the car and grew to the length of 35 mm. (Fig. 17.)

A small star-fish which was caught in the tow, and which set on June 28, was kept in the dish with many others until June 23. On this date it was placed in a small dish by itself and fed with small clams and barnacles. Fig. 23 shows the growth of this specimen: *a*, 2 mm., July 23; *b*, 4 mm., August 13; *c*, 4½ mm., August 18; *d*, 5 mm., September 6. On September 6 it was transferred to a car where there was an abundance of small barnacles. Fig. 23, *e* (12 mm.), represents size on September 26; *f*, 21 mm., on October 12; *g*, 30 mm., on November 5.

As a control of this experiment, several star-fish, which also set on June 28, were kept with a minimum amount of food. One of these, photographed at natural size on September 6, is shown in fig. 21 *a*, while the largest star in the car (with plenty of food) is represented in fig. 21 *b* (27 mm.). The specimen figured in *a* is 39 days old, and that in *b* is within a day or two of that age.

The next experiment (illustrated by fig. 22) on the growth of stars was as follows:

On August 3 two stars of average size were taken from the original car and placed in another car with a bunch of mussels.

On August 3 (No. 1) = 7 mm., fig. *a*. On August 16 (No. 2) = 10½ mm., fig. *a′*.

During this time the stars had little or no food, since they could not, or would not, eat the mussels. On August 15 a lot of barnacles was placed in this car, and by September 5 the results of the new food were evident enough:

September 5: (No. 1) = 15 mm., fig. *c* (one arm was torn off in measuring). (No. 2) = 19 mm., fig. *c′*.

September 26: (No. 1) = 28 mm., fig. *d* (new arm 10 mm. measured from mouth, growth of 7 mm.). (No. 2) = 29 mm., fig. *d′*.

October 12: (No. 1) = 36 mm., fig. *e* (regenerating arm, 20 mm., from mouth, growth of 17 mm.). (No. 2) = 41 mm., fig. *e′*.

From August 3 to August 16, while these specimens were not growing at all, those in the car grew about 6 mm. These two specimens afterwards, however, having more food and no interference in eating it, made up this difference, and by September 26 had grown as much as those in the original car.

One interesting point brought out by the experiment is that a star which is regenerating an arm may grow as fast as a complete star. Compare next experiment.

(*d*) *Rate of growth and rate of regeneration.*—The star-fish, like the lobster and many crabs, has the habit of dropping off an arm which has been mutilated and regenerating a new one. Unless the arm is mutilated or some other shock administered, one may sometimes tear a star in two by pulling on the arms, while the latter still remain on the fragments of the disk. On the other hand, if the suckers are cut off from one arm, or the arm is crushed or cut several times, it will usually drop off, always at the same point near the disk, taking the sexual glands with it.

On September 26 five of the larger stars in the original car were deprived of the arm opposite the "eye," or madreporic plate, and then placed in a car with barnacles for food. The subsequent measurements show that they kept on eating and growing at about the usual rate, like the specimen similarly treated in the last experiment described. The measurements are given in tabulated form below, the first measurement indicating the length of the longest arm.

Specimens.	Sept. 26.		Oct. 12.		Oct. 25.		Nov. 5.		Nov. 21.	
	Longest arm.	New growth.	Longest arm.	New growth.	Longest arm.	New growth.	Longest arm.	New growth.	Longest arm.	New growth.
A	32	0	36	3	42	7	41	11	40	12
B	30	0	35	3	38	7	41	12	40	11
C	28	0	30	3	35	7	38	10	38	12
D	27	0	29	3	30	6	35	9	38	11
E	25	0	28	3	....	....	34	7	35	9

A comparison of the table with that on page 217 shows that these stars which are regenerating an arm grew at about the same rate as the complete stars during the same period. The rate of regeneration was also about the same as the rate of growth in the original arms, except that toward the last the new members grew in some cases somewhat more rapidly.

Another experiment was made similar to the above, except that two arms were taken off instead of only one, and the stars were younger at the beginning. The stars were at first all about 12 mm. The eight detached arms were put in the car also, and on September 10, 26 days after they were detached, five were still alive and apparently in good health, but had neither grown nor shown any sign of regeneration. One is figured natural size in fig. 24 *b*.

The growth of these specimens is tabulated below. (Measurements were made from mouth to tip of new arm, but figures in table indicate merely new growth, and are derived by subtracting 3 mm. from original figures.)

Specimen.	Aug. 15.	Sept. 5.			Sept. 26.				Oct. 12.				Oct. 26.				Nov. 5.			
	Longest arm.	Longest arm.	First short arm.	Second short arm.	Longest arm.	First short arm.	Second short arm.	Newest arm.	Longest arm.	First short arm.	Second short arm.	Newest arm.	Longest arm.	First short arm.	Second short arm.	Newest arm.	Longest arm.	First short arm.	Second short arm.	Newest arm.
a	[1]12 (?)	22	....	8	34	18	17	....	42	32	30	....	....	....	....	....	....	....	....	....
b	12 (?)	20	....	7	30	17	17	....	36	26	26	....	....	....	....	....	43	31	31	....
c	12 (?)	18	....	5	25	[2]9	[3]9	....	37	16	15	....	....	....	....	....	40	24	24	....
d	12 (?)	18	....	5	23	14	12	[4]8	32	22	20	13	35	23	23	17	34	27	27	20

[1] It was intended at first to keep account only of rate of regeneration, and so four stars were picked out, of about the same size, and one only was measured. This was 12 mm. The others may have been 1 or 2 mm. larger or smaller. The growth of this specimen and the size of the single arm alone, on September 26, are given in diagram, fig. 24, *a* and *b* respectively.

[2] One detached arm, still alive, measures 7 mm.

[3] Tips cut off and arms slit on September 15. The longest arm was then 22 mm., and the regenerating arms 15 and 10 mm., respectively.

[4] Arm broken off, probably by handling, on September 5.

This experiment shows conclusively that when even two arms are lost the growth of the star-fish is not necessarily arrested or the rate of growth diminished. The rate of growth in the new arms was greater than in the original arms, and there was a tendency, therefore, for all to become ultimately of the same length.

The results show clearly that within very broad limits it is impossible to tell the age of a star-fish from its size. Star-fishes of all ages are able to live for months with very little or no food. The rate of growth depends directly upon the amount of food eaten. Star-fishes which are regenerating one, or even two, arms may, under ordinary circumstances, grow as rapidly as the complete stars. The growth of the new arms in the star-fish experimented upon was slightly more rapid than that of the original arms, showing a tendency in the organism to return to the original length In four months from time of setting, some of the larger stars kept in the cars under favorable circumstances attained a length of from 50 to 54 mm., or 2 to 2⅛ inches, measured from mouth to tip of arm. This is more than twice the length of many of the stars which were found just before the beginning of the breeding season, and which were therefore at least nearly a year old.

Allowing a moderate amount of growth during the winter and spring months, of 10 to 15 mm. (the amount of increase attained in one full month preceding October 12), the larger year-old star-fish in the early summer would be about 65 mm., or 2½ inches, in length, which is about the length of the greater number of stars taken on the mops in the Kickemuit River during the summer.

XI. *What is the size and age at sexual maturity?*

Among the star-fish caught in various parts of the bay on June 2, 3, and 4, several specimens only 1¼ inches, or 32 mm., were found to be very full of sexual products. This size was attained by many of the star-fish reared in the car on September 26, about three months from the time of setting. See table on page 217.* Great numbers of stars measuring about 2 inches, or 50 mm., were found ripe the first week of June. This was the size of several specimens in the car on October 25, which were not more than four months old, and whose sexual glands were well developed. In other words, a large number of the star-fish reared in the car were by the end of October as large as a great many which were sexually mature in June. Moreover, it was rare to find a specimen of this size on the 1st of June which was not full of ripe eggs, which were laid later, as the empty star-fish caught in July showed. It is an obvious conclusion, therefore, that, with fairly good opportunities to obtain food, the star-fish becomes sexually mature in less than a year, and that those hatched one season breed the next.

In his monograph on North American star-fishes, Alexander Agassiz gives his views with reference to their rate of growth in the following words (the figures referred to represent specimens, all of them smaller than that in our fig. 9, of a star about 2 weeks old raised in the car):

> The young star-fishes figured on this plate (pl. VIII) were all found attached to roots of Laminaria, thrown up on the beaches, in the neighborhood, after a storm; and from their different stages of growth, as compared with the oldest star-fish raised from a Brachiolaria (pl. VI, fig. 11), specimens of which were also found upon these roots, it is probable that the sizes here figured are 1 (fig. 1), 2 (fig. 8), and 3 (fig. 10) years old. A considerable number of specimens were picked up in this way, and they could all be arranged into very distinct groups, representing the star-fishes of the present and of two previous seasons. There seemed to be no gradation from one group to another, such as we have among the young sea-urchins, which, in consequence of their manner of breeding during the whole year, form series the relations of which it is impossible to determine. In this connection I would say that by arranging the star-fishes found upon our rocks into series according to their size we are able to obtain a rough estimate of the number of years required by them to attain their full development; this I presume to be somewhere about fourteen years.† They begin to spawn

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* Eggs from a specimen of 38 mm. were readily fertilized with spermatozoa from a male of same size.

† For an account of the method adopted by Professor Agassiz for ascertaining the age of many of our marine animals, see Proceed. Essex Inst., 1863, p. 252.

before that time, as specimens have been successfully fecundated which evidently were not more than six or seven years old. It is during the fourth year that the rate of growth seems to be most rapid. A young star-fish, measuring 1½ inches across the arms, was kept during five months alive in Mr. Glen's tank at the museum, and during that space of time it grew to 3 inches.

It will readily be seen that my observations do not agree with those of Agassiz. I found no difficulty in obtaining all possible gradations in size among the stars in the late summer, and those represented by Agassiz as 1, 2, and 3 years old, respectively, more nearly correspond with those raised in cars when they were 1, 2, and 3 weeks old.

XII. *What are the natural enemies of the star-fish?*

The destructive agents and natural enemies referred to in the last report were cold and fresh water, various fishes which feed upon the larvæ, gulls and crows, and parasites. Some specimens which were attacked by the parasite frequently found in the fall of 1897 were kept over winter, and by spring the disease had disappeared; but the effects of the disease were sometimes visible. In one case an arm was entirely eaten through, about ¾ inch from the tip, but was not thrown off. The stump healed over, and the star was kept throughout the year. It showed almost no trace of regeneration, probably because food was rarely taken by the specimen.

The enemy which is doubtless the most destructive to the star-fish is the menhaden. In an article on the "Food of the menhaden," published in the United States Fish Commission Bulletin for 1893, Dr. James I. Peck showed that this fish feeds exclusively upon the minute organisms which swim or float free in the water. The open mouth of the menhaden has an area of about a square inch, and as the fish swims through the water with open mouth and gill-covers raised, a considerable column of water is passed through the mouth every minute (estimated by Dr. Peck at about 7 gallons). The gillrakers strain the water, and the organisms which are not too minute are caught in the mouth and swallowed. The star fish larvæ, of even small sizes, are far too large to pass through the gillrakers. Numerous schools of menhaden feed in our bay during the season when the star-fish larvæ are swimming at the surface, and undoubtedly destroy them by thousands of millions.

After the stars are set they are no longer in danger of being destroyed by the menhaden, but for several weeks are bright conspicuous objects upon the seaweed and eelgrass for eels and many small fishes to feed upon.

XIV. *Is the popular idea that the dismembered fragments of a star-fish will regenerate new star-fish founded on fact?*

This idea is commonly held, and is apparently founded on the fact that in nearly every lot of stars brought up in the dredges or on the mops a considerable number may be found which are regenerating lost parts. Frequently two, three, or even four arms are being regenerated, and these are much smaller than the original arms. Upon careful examination and inquiry into the extent of this regeneration I have never found a well-authenticated case among our species of stars in which part of the disk was being regenerated, except those reared with great care in the aquarium. With this point in view I have examined a large number of regenerating stars caught in their natural haunts, some of them reported to be regenerating part of the disk, but invariably the regeneration was limited to the arm. I have, however, made a few experiments in the aquarium and in the cars which have a bearing upon this question.

The fact that a mutilated arm is frequently loosened and dropped off at a particular point near the base and the rate of regeneration of specimens which have thus lost one or two arms are recorded previously (p. 219).

All of the arms may be pulled off and if the star is protected and fed all will regenerate. Such a specimen is sketched in fig. 25. This specimen was kept after the operation in a glass dish with frequent changes of water, and was fed upon the soft parts of crabs, etc. The regeneration was slow as compared with that given in the previous tables, the new growth shown in the figure (which is natural size) requiring five or six weeks, probably owing to the comparatively small amount of food taken.

Since a mutilated arm drops off from the disk so readily, the latter nearly always remains intact, and in ordinary cases, therefore, if two stars were to result from one, one of them must regenerate from a single arm. I have several times kept single arms for a long time in the aquarium or cars, but have never seen any trace of regeneration in them. On May 11 several arms were taken off at the usual line of detachment, and kept alive in the aquarium until June 9, when they showed no sign of regeneration. One of these was still alive on June 25, and at that time was apparently enjoying good health, and would turn over if put on its back. It had lived, therefore, for over six weeks, but showed no signs of regeneration.

Another experiment was started on August 15; two arms were taken off from each of four specimens. The rate of regeneration of these specimens is given in the tables on p. 219. On September 10, nearly three weeks afterwards, five of the single arms were found alive, but showed no regeneration. On September 5 the new growth in the arms regenerating from the disk was from 8 to 5 mm. On September 26, six weeks after the operation, one of the single arms was found alive (7 mm.) It had not shown any traces of regenerating a new arm, although it had healed. This arm is represented natural size in fig. 24, *b*, and the new growth which took place on one of the stars from which these arms were detached is shown in fig. 24, *a*. Similar experiments were tried last year with the same result. In a recent article by Miss Helen Dean King, in Roux's Archiv, it is stated that single arms were kept alive for two weeks, but never showed signs of regeneration.*

Several experiments were carried on to determine what regeneration would take place if the disk were cut through. On the 11th of May 19 specimens about 2½ inches in length were treated in the following manner: Two arms were pulled off, and at the base of one of the arms a piece was cut out from the top of the disk in the manner shown in fig. 26. These specimens were placed in a large car at Woods Hole without food (except what could be carried in the water). On June 9 there was a trace of regeneration in some of the arms. On June 25, a little more than six weeks after the operation, all the arms were growing out anew, and varied from a mere trace of a new arm with the terminal eye-spot (which always shows first) to arms ¼ inch (about 7 mm.) long. This experiment shows two things: that the new arm will regenerate if a portion of the disk is absent, and that the rate of regeneration, like the rate of growth, in normal specimens, is dependent upon the nourishment, for while the new growth in these cars was only 7 mm. in six weeks, those which were well fed at Kickemuit gained a new growth of from 13 to 18 mm. in the same time. See page 217.

Other experiments were tried, to determine what regeneration would take place if the whole star-fish were cut through in various ways, while the arms were left in place. It will be seen that the results were not always the same.

In the summer of 1897 several stars about 2½ inches in length were cut through so as to leave three arms and part of the disk on one piece and two arms and part of the disk on the other. The smaller pieces perished, but the larger ones lived for several weeks and showed no sign of regeneration. All but one were destroyed by other star-fishes which got into their compartment of the car by accident. The remaining fragment, consisting of three arms and part of the disk, lived several months after the operation and did not regenerate.

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* During the summer of 1899 several single arms were kept alive from early in May until the middle of August, when they were destroyed by accident. There was no regeneration.

On May 11, 1898, several stars about an inch long were cut as in fig. 27. One arm was pulled off and the disk then cut in two, leaving two arms with a part of disk and madreporic plate on one piece (= *a*), and two arms and part of disk on the other piece (= *b*). The fate of the single arm has been already considered (page 222). On June 9 all the pieces were alive. In the piece marked *a* (i. e., having madreporic plate) a trace of a new arm was visible on the side toward the lost arm, but in no other place. The pieces marked *b* showed no regeneration at all.

On June 25, 6½ weeks after the operation, the condition was as follows: All these parts of specimen 1 were alive. The fate of the single arm has been mentioned previously. The piece (*a*) with madreporic plate is sketched from the lower side in fig. 28. Two arms were well started and one minute arm was growing out between them. In the other piece (*b*) of this specimen, the wound was completely healed, but there was no visible trace of any new arms. Of specimen 2, only one piece (*a*) was alive. From the stump of the old arm a very small new arm appeared—no trace of any other. The two pieces *a* and *b* of specimen 3 were alive and healthy. In *a* two very small arms were visible (one could be seen only with the help of a hand lens) near together, and on one side of the cut surface; on the other side there was a trace of another arm, indicated by an eye-spot. *b* had healed up, but showed no trace of regenerating arms. Of the fourth specimen, piece *a* was alive with two very minute regenerating arms. These specimens had very little food, and it is hardly necessary to remark that they grew very little or not at all.

On September 5, 1898, another experiment, similar to the last, was commenced at Kickemuit River. Eight specimens were taken from those reared in the car and cut in two in the manner shown in fig. 29, leaving two arms and the madreporic plate on one piece and three arms and part of the plate on the other. The pieces of the latter sort died in a short time, and the following data refer to the pieces having two arms and the plate ("eye"). At the beginning of the experiment the specimens measured in millimeters, 23, 21, 21, 20, 19, 18, 18, 18.

September 26, 3 weeks after the operation:
- A, 22 mm., bore trace of two new arms.
- B, 18 mm., two new arms (preserved) unhealthy.
- C, 18 mm., one new arm, 2 mm.
- D, crushed.
- E, 20 mm., healthy; no trace of another arm.
- F, overlooked. See next, Oct. 12.

October 12:
- A (?), 23 mm., two very small arms.
- C, 20 mm., two arms, one smaller than the other.
- E (?), 22 mm., no trace of regeneration.
- F, 21 mm., one arm.

(all healthy.)

October 25:
- C, 20 (?), two arms 8 to 10 mm.; no trace of other.
- E, 22, no trace of regeneration.
- F, $\left\{\begin{matrix}21\\20\end{matrix}\right.$ (?), one arm, 6 mm.; no trace of another.

November 5:
- A, 25 mm., two new arms, 2 mm. each.
- C, 21 mm., two new arms, 9 to 10 mm.: no trace of other.
- E, 22 mm., one new arm directly in middle, 1 mm. long.
- F, 19 (?), one arm, 4½ mm.; no trace of rest.

November 11 (fig. 30):
- A, 23 mm., two small arms, about 3 mm.
- C, 21 mm., two small arms, 10 and 12.
- E, 21 mm., one arm, 1½ mm., directly in middle.
- F, 20 mm., one arm, 6 mm.

(no trace of other arms in any.)

Similar experiments upon young stars about the first of August yielded essentially the same results, except that out of seven pieces which lived until September 5 four were without madreporic plate and three of these were regenerating new arms. Miss King, whose recent article has been already referred to, seems to have had better success than I, and says that from each of the pieces of a star cut in two a new star may be formed by regeneration. That the madreporic plate is not essential to the life of the star, at least for a very long time, is shown by another experiment: This organ was removed from five large stars on June 14, and on November 5 one of them was alive and healthy, but had not regenerated the lost structure. The madreporic plate was wanting in a specimen caught at Woods Hole on April 4. Another was taken which had an accessory madreporic plate, which was not, however, connected with the stone canal. In the last report I mentioned an experiment in which this body was extirpated and regenerated before the end of the season.

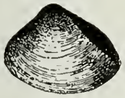
In every known case of regenerating star-fish caught on the mops and dredges the new growth is limited to the arms. The arms are readily loosened and cast off when injured, but almost certainly do not produce new stars, as is shown by the experiment in which single arms have been kept three months without trace of regenerating, and by the fact that single arms regenerating the rest of the stars have never been found among this species of star (they are common in some foreign species). Star-fish which have been cut in two behave differently in different cases. They may live for a long time without regenerating the remaining arms to the slightest degree; they may show no sign of regeneration for several weeks and then regenerate one or more arms; they may soon regenerate only one or two of the arms when three are required to complete the original form of the body. The rate of regeneration and perhaps the possibility of regeneration are, like the rate of growth, dependent on the food supply. It is probably possible for two or more complete stars to result from one, but in many experiments in which the stars were carefully protected this result has not been obtained by me. The probability of this result occurring when stars are torn apart and thrown overboard is doubtless very slight, for, as the experiments show, such stars have difficulty in obtaining food and are especially liable to injury and to destruction by other stars or enemies of various kinds.

XV. *What are the artificial methods of destruction now in use in Rhode Island or elsewhere?*

Star-fishes are caught in considerable numbers with the spear and tongs, but the more efficient method is the use of the "tangle" or "mop." The tangle consists of a number of mops of cotton waste or similar material attached to an iron bar. By dragging these mops over the oyster-beds the stars become entangled and are drawn up with the mops. The mops are usually detached from the iron bar and are thrown, together with the stars, into a tub of hot water. Meanwhile other mops are attached to the bar and thrown overboard. After the stars are killed they can be more easily picked off the mops than when they are alive. Some oystermen prefer to dredge up oysters, stars and all, and, after having culled out the stars, to replant the oysters.

The star-fish become easily entangled in the mops, not only because they are rigid and covered with spines, but because the little forceps (pedicellaria) thickly scattered over the surface of the body catch hold of the threads of the mop. If one presses the upper surface of a live star-fish against the back of his hand he will find that these pedicellaria grasp the hairs on the hand tightly and will sustain the whole weight of the star-fish.

PLATE 23.



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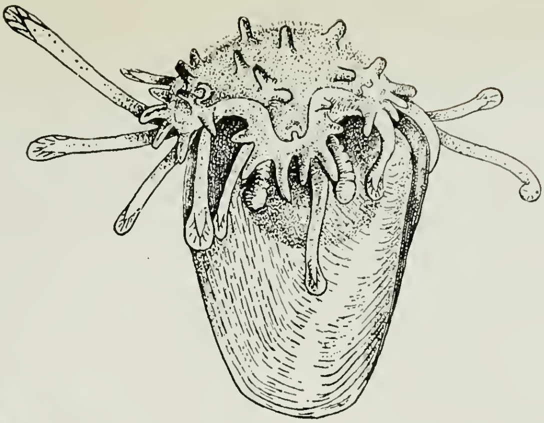

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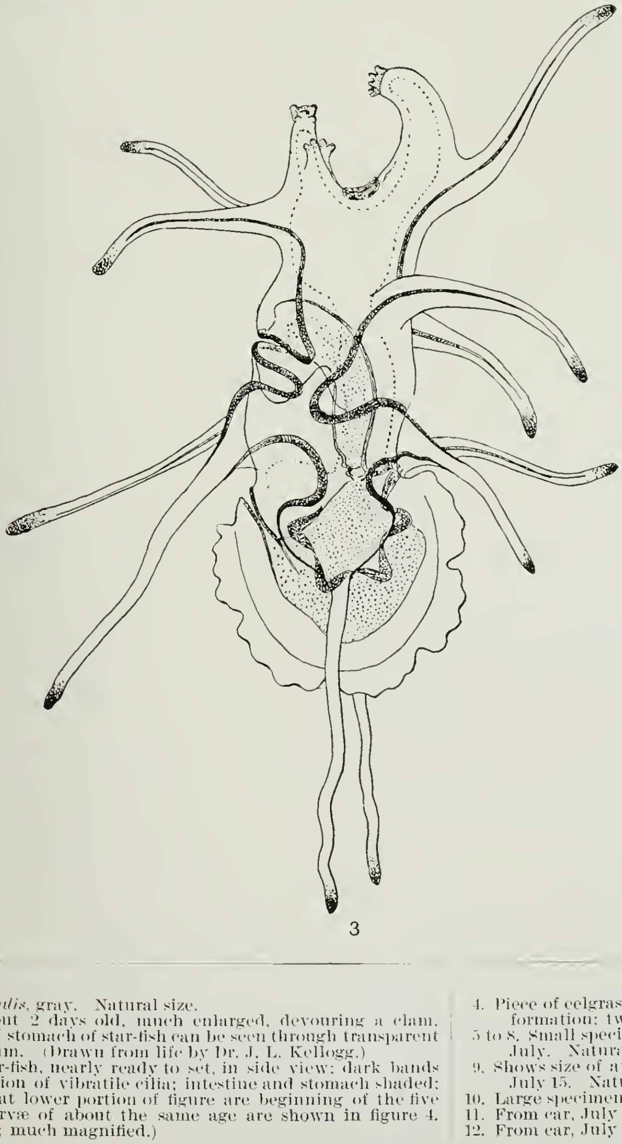

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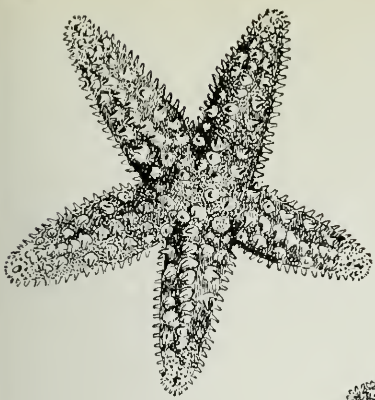
12

1. *Mulinia lateralis*, gray. Natural size.
2. Star-fish about 2 days old, much enlarged, devouring a clam. Outlines of stomach of star-fish can be seen through transparent shell of clam. (Drawn from life by Dr. J. L. Kellogg.)
3. Larva of star-fish, nearly ready to set, in side view: dark bands show position of vibratile cilia; intestine and stomach shaded; five lobes at lower portion of figure are beginning of the five arms. Larvæ of about the same age are shown in figure 4. (From life; much magnified.)
4. Piece of eelgrass with star-fish larvæ just undergoing their transformation: two larvæ at sides. Natural size.

5 to 8. Small specimens of star-fish from seaweed, about the first of July. Natural size.

9. Shows size of average star found upon eelgrass and seaweed, on July 15. Natural size.
10. Large specimen from car, July 15. Natural size, 3 mm.
11. From car, July 18, large specimen, 5 mm. Natural size.
12. From car, July 24, large specimen, 8 mm. Natural size.

PLATE 24.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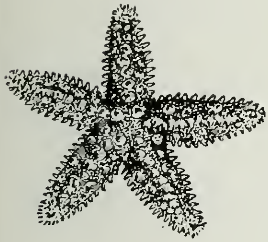
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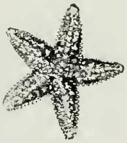
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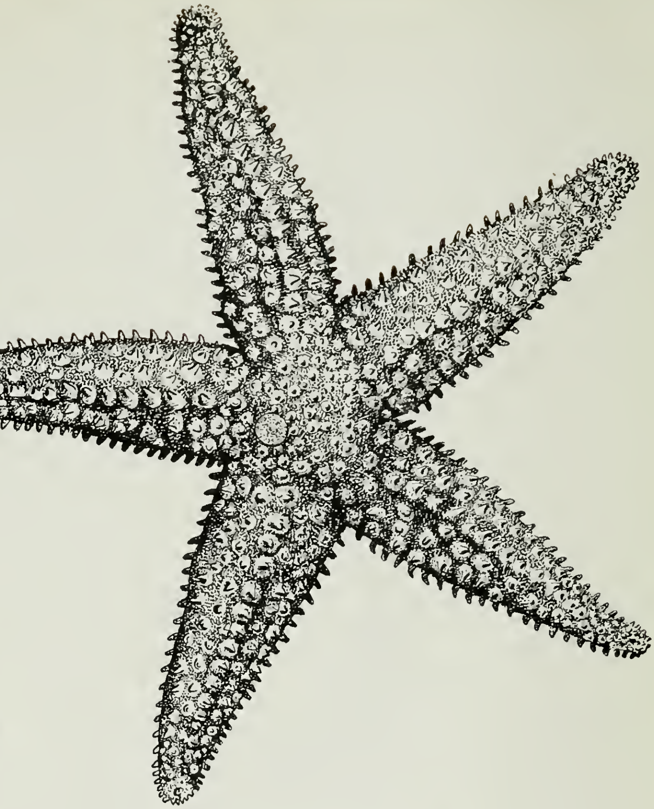
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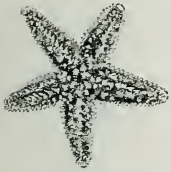
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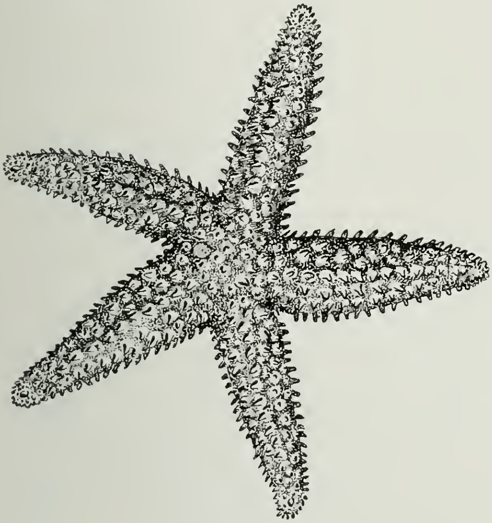
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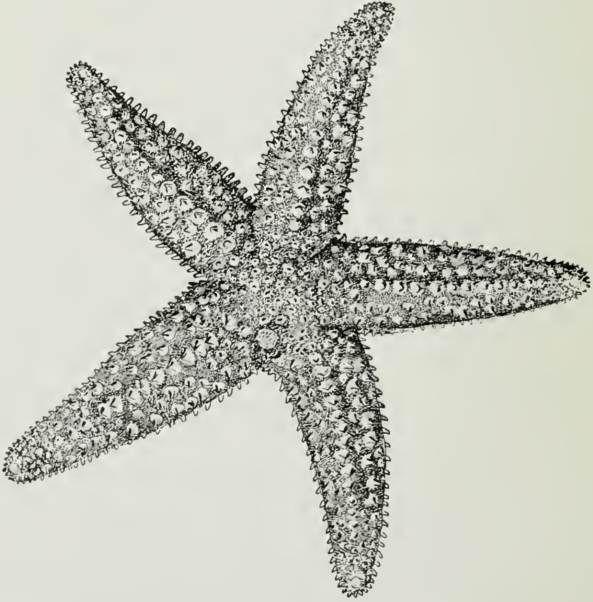
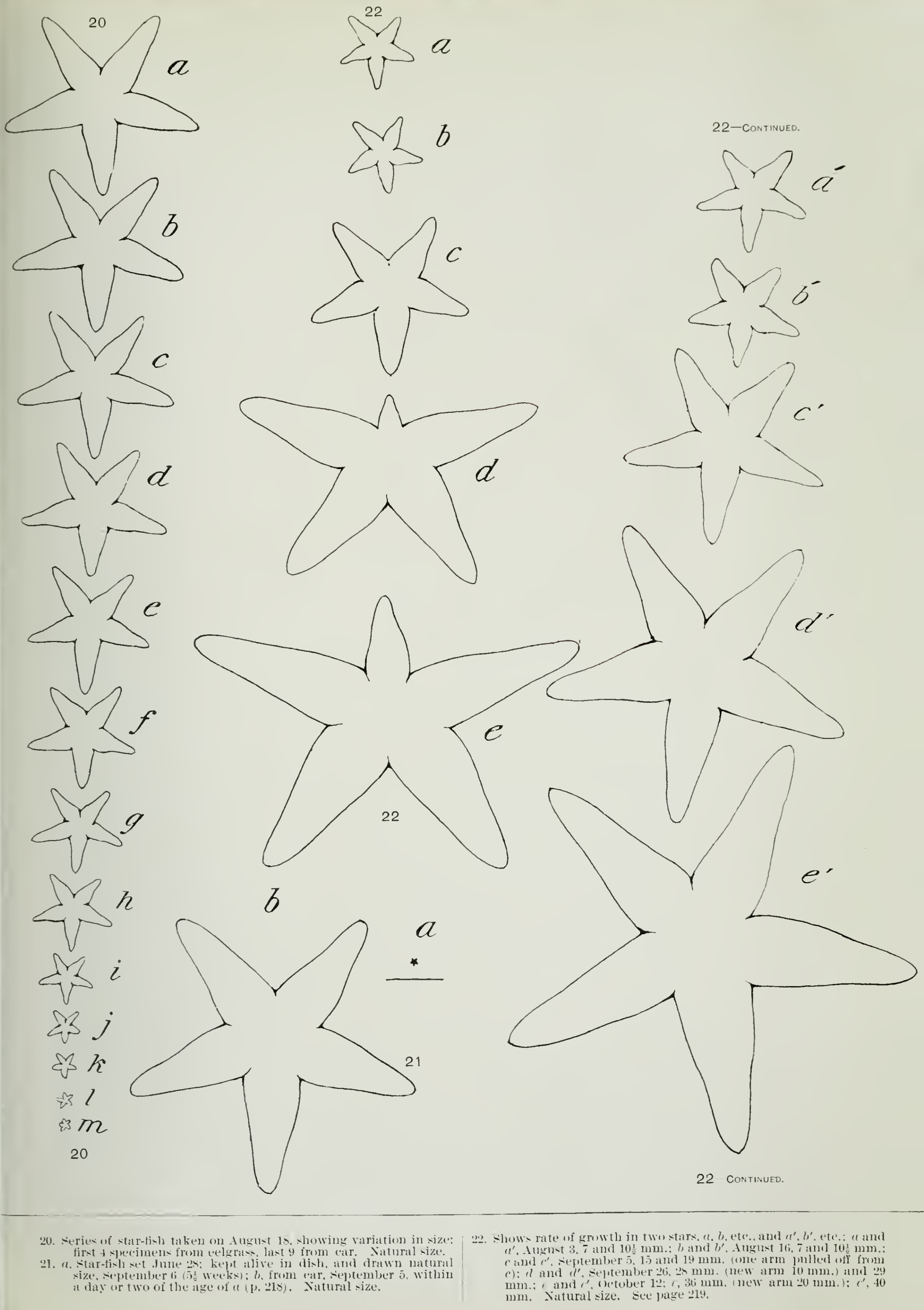

18

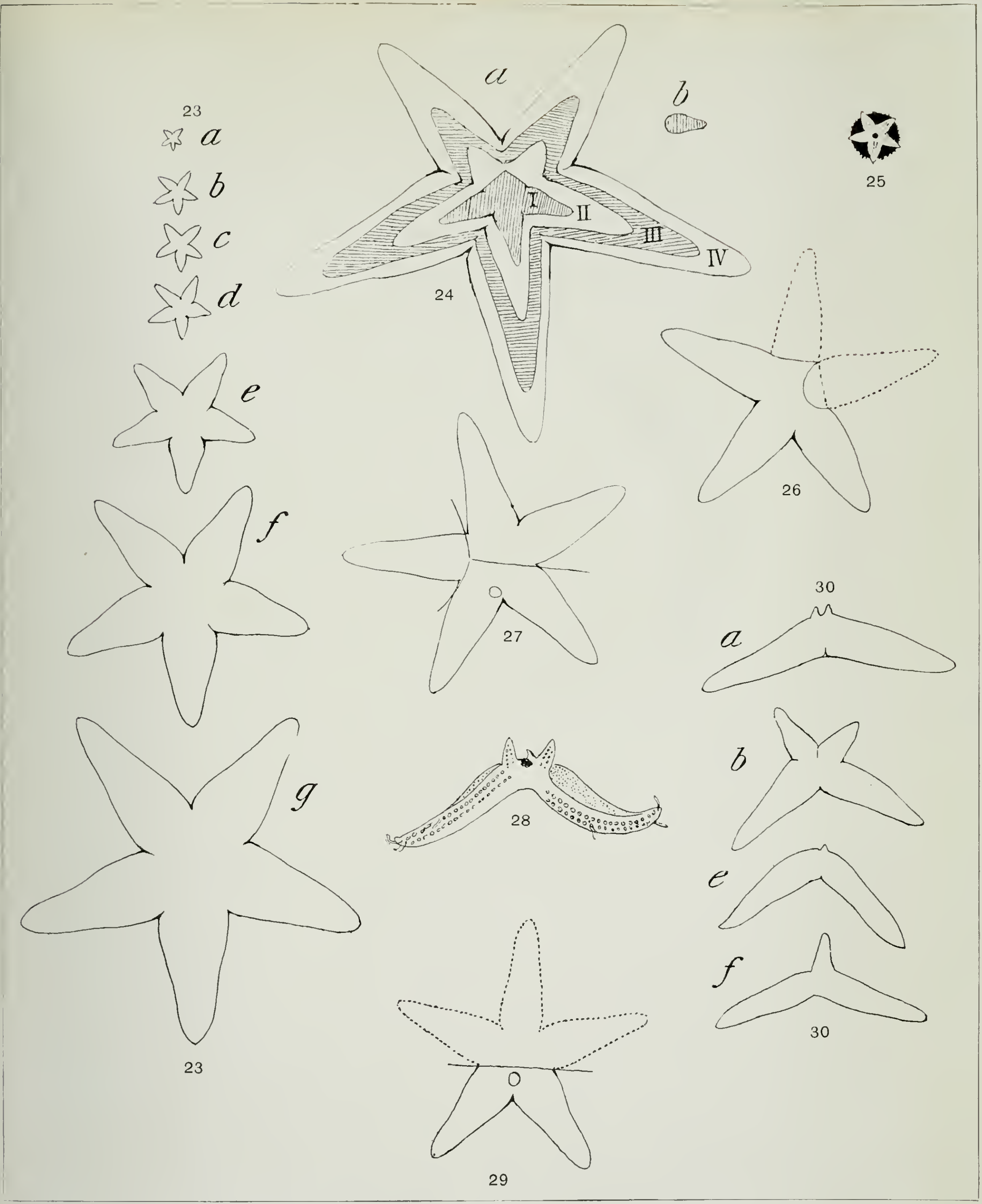
13. From car, July 26, large specimen, 9 mm. Natural size.
14. From car, August 2, large specimen, 11 mm. Natural size.
15. From car, August 18, large specimen, 18 mm. Natural size.
16. From car, September 5, large specimen, 24 mm. Natural size.
17. From car, September 26, large specimen, 35 mm. Natural size.
18. From car, October 12, large specimen, 42 mm. Natural size.
19. From car, October 25, largest specimen, 54 mm. Natural size.



20. Series of star-fish taken on August 18, showing variation in size: first 4 specimens from eelgrass, last 9 from car. Natural size.

21. *a*, Star-fish set June 28; kept alive in dish, and drawn natural size, September 6 (5½ weeks); *b*, from car, September 5, within a day or two of the age of *a* (p. 218). Natural size.

22. Shows rate of growth in two stars, *a*, *b*, etc., and *a′*, *b′*, etc.; *a* and *a′*, August 3, 7 and 10½ mm.; *b* and *b′*, August 16, 7 and 10½ mm.; *c* and *c′*, September 5, 15 and 19 mm. (one arm pulled off from *c*); *d* and *d′*, September 26, 28 mm. (new arm 10 mm.) and 29 mm.; *e* and *e′*, October 12; *e*, 36 mm. (new arm 20 mm.); *e′*, 40 mm. Natural size. See page 219.



23. Shows growth of single specimen collected as a larva and set June 28. *a*, July 23, 2 mm.; *b*, August 13, 4 mm.; *c*, August 18, 4½ mm.; *d*, September 5, 5 mm.; *e*, September 26, 12 mm.; *f*, October 12, 21 mm.; *g*, November 5, 30 mm. Natural size. See page 218.

24. *a*, Rate of growth and of regeneration: I, August 15; II, September 5; III, September 26; IV, October 12; *b*, single arm alive, from August 15 to September 26. Natural size. See page 219.

25. Star regenerating five arms from ventral side. Natural size. See page 222.

26. Showing manner of cutting the stars in the experiment described on page 222.

27. Showing manner of cutting the stars in the experiment described on page 223.

28. Showing the regeneration of the arms in the experiment described on page 223; a portion of the disk regenerating three arms. Natural size.

29. Showing manner of cutting the stars in the experiment described on page 223. Natural size.

30. The result of one of the regeneration experiments described on page 223; one or two arms regenerating from a part of the disk. Natural size.

THE REAPPEARANCE OF THE TILEFISH.

By H. C. BUMPUS.

U. S. Fish Commission Bulletin for 1898.

U. S. COMMISSION OF FISH AND FISHERIES,
GEORGE M. BOWERS, Commissioner.

CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION, WOODS HOLE, MASSACHUSETTS.

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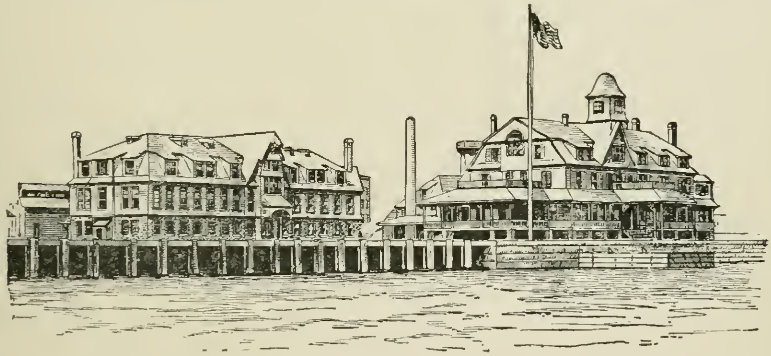
BY

HERMON C. BUMPUS, Ph. D.,
Director of Biological Laboratory of United States Fish Commission.



Extracted from U. S. Fish Commission Bulletin for 1898. Pages 321 to 333.

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1899.

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Woods Hole, Massachusetts.

THE REAPPEARANCE OF THE TILEFISH.

By HERMON C. BUMPUS, Ph. D.,
Director of Biological Laboratory of United States Fish Commission.

During the past summer the investigations of the United States Fish Commission have brought to light the facts that the tilefish (*Lopholatilus chamæleonticeps*), once supposed to be extinct, occurs in great numbers off the southern coast of New England, and that its capture requires only the ordinary apparatus used in cod and haddock fishing. This fish possesses excellent food qualities and its reappearance may result in the development of an industry of considerable importance. Its history is of scientific interest, since it furnishes evidence that life on the sea bottom is subject to periodic modification, and that a species almost annihilated may become quickly reestablished.

In May, 1879, Captain Kirby, of Gloucester, in command of the schooner *William V. Hutchins*, while searching for cod and hake almost directly south of Nantucket, caught great numbers of a "strange and handsomely colored fish." The first catch, of nearly 2,000 pounds, was made in water varying from 80 to 120 fathoms in depth, at latitude 40° 04′ N., longitude 70° 23′ W. Four trawls were used, each about a mile in length, and bearing 1,000 hooks. Nearly all of these fish were thrown overboard, but a few were kept and cooked.

Captain Kirby stated that they were the finest fish he had ever eaten, and he determined to save and salt all that he might catch. The trawls were set the same day in latitude 40° 04′ N., longitude 70° 17′ W., and again in latitude 40° 00′ N., longitude 70° 04′ W. Both sets yielded about 2,000 pounds of dressed fish, which, on being landed in Gloucester, were sold to Messrs. Friend & Son, who disposed of them in various ways.

Captain Kirby sent one of the fish to the United States National Museum, where it was examined by Messrs. Goode & Bean, and described (Proceedings U. S. Nat. Mus., vol. II, pp. 205–208) as a new genus and species (*Lopholatilus chamæleonticeps*). Recently it has been assigned by Jordan & Evermann to the family *Malacanthidæ*, a group of fishes of somewhat obscure relationship, found in temperate and tropical seas.

In July of the same year Captain Dempsey, also of Gloucester, caught 9 tilefish while fishing for cod in a locality 50 miles south by east of No Man's Land, in 75 fathoms of water.

Professor Baird took great interest in the discovery of this new fish. Its fine flavor and attractive appearance indicated excellent marketable qualities, and its great abundance promised to be a profitable source of income to offshore fishermen.

The *Fish Hawk* took 3 specimens on the 13th of September, 1880, in 126 fathoms, latitude 39° 57′ N., longitude 70° 56′ W., and so anxious was Professor Baird to gain additional information that he chartered the fishing smack *Mary Potter*, of Noank, in which Mr. Vinal Edwards left Newport for the tilefish grounds on the 29th of September. A trawl line of 400 hooks, baited with menhaden, was set in 127 fathoms, but only a swordfish and two skates were caught. Threatening weather then drove the vessel back to port.

On August 9, 1881, trawl lines were set from the *Fish Hawk* in 134 fathoms, latitude 40° 02′ N., longitude 71° 12′ W., and 8 tilefish, weighing 147 pounds, were taken. On August 23, in latitude 40° 03′ N., longitude 70° 31′ W., 73 fish, weighing 540 pounds, were taken. The trawl line was set again on September 21 at a point farther to the eastward, latitude 39° 58′ N., longitude 70° 06′ W., in water of 113 fathoms, but no fish were taken.

In March and April, 1882, vessels entering New York and other Atlantic ports reported that they had passed through countless numbers of dead fish while crossing the northern edge of the Gulf Stream. Investigation proved that these were tilefish, and that they appeared on the surface of the water over an area of 170 miles in length and 25 miles in width. A conservative estimate, made by Capt. J. W. Collins (Fish Commission Report for 1882), who has given a detailed history of the tilefish up to the time of this mortality, placed their number at upwards of 1,438,720,000. Allowing 10 pounds to each fish, he has estimated that there would be 288 pounds of fish for every man, woman, and child in the United States.

In September, 1882, Professor Baird chartered the *Josie Reeves*, and sent her to the tilefish grounds, that he might ascertain to what extent the species had been depleted, but the vessel returned without having found a single individual. This seemingly unprecedented destruction of marine life was extensively commented upon both by newspapers and scientific journals, and in the Report of the U. S. National Museum for 1889 the tilefish was placed, provisionally, in a list of extinct animals.

The scientific work that finally led to the rediscovery of the animal really began in the summer of 1880, when the completion and equipment of the *Fish Hawk* made it possible to enter upon lines of investigation which before were out of the question. This vessel has added materially to the practical efficiency of the Commission, and its frequent employment by men of science has greatly increased our knowledge of oceanic life.

In November, 1880, Professor Verrill published his memorable "Notice of the remarkable marine fauna occupying the outer banks of the southern coast of New England" (Am. Jour. Sci., Nov. 1880, p. 390), in which he gave the scientific results of three excursions made by the *Fish Hawk*. On these excursions the dredge was used 23 times, and an enormous number of deep-sea animals were taken. Among these were 130 species of mollusks, 26 echinoderms, 43 crustacea, and 16 fish new to the southern coast of New England, and many of these animals were also new to science.

During the following summer, 1881, seven excursions were made to the Gulf Stream, where, besides the work done with the line trawl already mentioned, the dredge was used 47 times. It is fortunate that these investigations were made in 1880 and 1881, since they furnished definite data respecting the physical and biological conditions of a tract of the sea bottom which in the spring of 1882 became the scene of widespread devastation.

While Captain Collins was collecting his data, the *Fish Hawk*, which had taken a few tilefish in 1880, and had found them very numerous in 1881, was continuing her deep-sea explorations under the direction of Professor Verrill. During August, September, and October, 1882, five trips were made to the tilefish grounds, and the dredge was lowered 46 times. The definite information relative to the life on the sea bottom, which Professor Verrill had been able to secure during the summers of 1880 and 1881, now became of great value, since it enabled him to report on the general faunistic changes which had affected this area, to measure the extent of the destruction of oceanic life, and to give an intelligent reason therefor.

In the report for 1882, he writes:

> One of the most peculiar facts connected with our dredging this season (1882) was the scarcity or absence of many of the species, especially crustacea, that were taken in the two previous years, in essentially the same localities and depths, in vast numbers, several thousand at a time.

In another article (Physical characters of the portion of the continental border beneath the Gulf Stream, explored by the *Fish Hawk*, 1880 to 1882), Professor Verrill describes the rapid incline of the sea bottom beyond the 100-fathom line, "usually as steep as the side of a great mountain chain, and about as high as Mount Washington, New Hampshire." He further writes:

> The bottom along the upper part of this slope and the outermost portion of the adjacent plateau, in 65 to 150 fathoms, and sometimes to 200 fathoms or more, is bathed by the waters of the Gulf Stream. Consequently the temperature of the bottom water along this belt is decidedly higher than it is along the shallower part of the plateau near the shore, in 25 to 60 fathoms. * * * We may therefore call the upper part of the slope, in about 85 to 150 fathoms, the "warm belt."—(Report U. S. Fish Commission for 1882, p. 279.)

It was along this warm belt that many animals characteristic of tropical or subtropical fauna were dredged in 1880 and 1881, and Professor Verrill states:

> In fact, this belt is occupied by a northern continuation of the southern or West Indian Gulf-Stream fauna * * * that could not exist there if the Gulf Stream did not flow along this area at the bottom, both in winter and summer.

The tilefish, whose relatives are known to be tropical, doubtless belongs to this warm-water fauna, and the destruction of 1882 was explained by Professor Verrill when he wrote, in October of that year:

> It is probable, therefore, that the finding of vast numbers of dead tilefish floating at the surface in this region last winter was connected with a wholesale destruction of the life at the bottom, along the shallower part of this belt (in 70 to 150 fathoms), where the southern forms of life and higher temperature (47° to 52°) are found. This great destruction of life was probably caused by a very severe storm that occurred in the region at that time, which, by agitating the bottom water, forced outward the very cold water that even in summer occupies the wide area of shallower sea in less than 60 fathoms along the coast, and thus caused a sudden lowering of the temperature along this narrow warm zone, where the tilefish and the crustacea referred to were formerly found.
>
> The warm belt is here narrow, even in summer, and is not only bordered on its inner edge, but is also underlaid in deeper water by much colder water. In fact, the bottom water inshore is probably below 32° F. in winter where the depth is 20 to 40 fathoms. In August this year (1882) we found the temperature 37° F., south of Cape Cod, in 55 to 60 fathoms. It is evident, therefore, that even a moderate agitation and mixing up of the warm and cold water might in winter reduce the temperature so much as to practically obliterate the warm belt at the bottom. But a severe storm, such as the one

> referred to, might even cause such a variation in the position and direction of the tidal and other currents as to cause a direct flow of the cold inshore waters to temporarily occupy the warm area, pushing farther outward toward the Gulf-Stream water. The result would in either case be a sudden and great reduction of temperature, perhaps as much as 15° to 20°. This could not fail to be very destructive to such southern species as find here nearly their extreme northern limits. It is probable, however, that these southern species, including the tilefish, were not thus destroyed farther south. Therefore it is probable that in a few years they will again occupy these grounds by migrating northward, even if there be not enough left here to replenish their races.—(Report of the United States Fish Commission, 1882, p. 279.)

These quotations are here inserted because they are based on facts ascertained by those interested in the scientific work of the Commission and because they explain adequately the cause of the mortality, ascribing it to climatic changes.*

In 1883 the *Fish Hawk* made but one excursion to the Gulf Stream, and even then did not reach the edge of the "warm belt," the deepest water in which the dredge was cast being only 62 fathoms. The *Albatross* worked on the ground, however, and cast the dredge at least 20 times over the area known to have been occupied previously by the tilefish. Since 1883, up to the present time (January, 1899), the *Fish Hawk* has not again attempted to explore this portion of the sea bottom.

In 1884 the *Albatross* made a most careful survey of the "tilefish grounds" and the tracts of deeper and shallower water bounding the same. The dredge was lowered 76 times, and although material of great scientific interest was secured, no trace of the tilefish was found.

In 1885 the examination of the sea bottom in this locality was continued, and the dredge was lowered from the *Albatross* 38 times.

In 1886 the *Albatross* lowered the dredge 14 times, but no tilefish were found.

It is worthy of note that the first cruise made by the Fish Commission schooner *Grampus* was to the tilefish grounds. The vessel left Newport on August 14, 1886, and set trawls in 96 fathoms (latitude 39° 59′ N., longitude 70° 15′ W.), and although trawls and hand lines were repeatedly used until August 21 the ground was so barren that only a few hake were taken. The stomachs of these fish showed a scarcity of food suitable for the *Lopholatilus*, and Captain Collins concluded that—

> It is safe to say that the large number of sets made with the trawl line on this occasion, together with the trials made with hand lines, clearly demonstrate the fact that if the tilefish has not become absolutely extinct in this region it is certainly so rare that the chances of obtaining it are limited.

In 1887 the *Albatross* made three unsuccessful efforts to find the tilefish, and in November left the Atlantic waters and sailed to the Pacific, where she has remained.

In 1888 no attempt was made to visit the tilefish ground.

In 1889 Prof. William Libbey, jr., began a series of temperature and specific-gravity observations off the shore of southern New England, which extended directly over this interesting tract. These observations were made for the purpose of "establishing some connection between the changes in temperature in the waters and the migrations of the fish which inhabit them." The *Grampus* was placed at the disposal of Professor Libbey, and an account of his work for the summer of 1889 will be found in the U. S. Fish Commission Bulletin, vol. IX. This account contains a record of over 1,600 temperature observations, and the general results were of such importance that Commissioner McDonald continued the work during the summer of 1890, at which time the United States Coast Survey steamer *Blake* was detailed to act in cooperation with the *Grampus*.

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*Professor Libbey, in a paper read before the Geographical Congress in 1895, claims that the effect of any single storm is largely superficial, and that it takes the resultant of several years of storms permanently in one direction or the other to produce such effects in deep water. Professor Libbey ascribes the disappearance of the fish to conditions just the reverse of those mentioned by Professor Verrill, namely, the cold body of water on the continental platform was allowed to advance over the area upon the edge of the continental plateau by a retrogression of the warm waters of the Gulf Stream produced by the exact opposite of the conditions which caused its advance toward the same edge.

During the summer of 1891 the *Grampus* was placed again at the disposal of Professor Libbey, and the work was continued along the same lines as during the two previous years. Unfortunately, the results of these investigations, perhaps the most complete ever conducted over a tract of the ocean of equal extent, have never been published, although they yielded extremely important data relative to the physical changes affecting the sea and the sea bottom. Professor Libbey found that a comparison of the temperature records as shown by the temperature cross-sections constructed upon the basis of the observations made in this body of water for the three years 1889, 1890, and 1891, demonstrated that there had been a progressive movement of the warm water, of 50° temperature, toward the shore.

In a communication addressed to Commissioner McDonald in 1892, Professor Libbey wrote:

> In 1889 the lower portion of the curve did not touch the edge of the continental platform at any point within the area we were studying. In 1890 this portion of the curve touched the continental edge both at Block Island and off Nantucket Island in the latter part of the season; and in 1891, as has been said, it touched along the whole edge of this portion of the platform during the greater part of the summer. The change which was thus produced in the temperature at the bottom along this edge of the continental platform was in the neighborhood of 10°, an item of considerable importance.—(Report U. S. Fish Commission, 1893, p. 34.)

Professor Libbey, in a conference with Commissioner McDonald, showed that if the movement of the warm band toward the shore continued during the summer of 1892, the whole of the continental edge, or that part of it upon which the tilefish had once flourished, would present environmental conditions favorable to the return of the fish. The importance of these presentations was recognized by Commissioner McDonald, and though other work had been laid out for the *Grampus*, she was ordered to prepare for further explorations of the Gulf Stream and the bottom fauna off the southern New England coast. Professor Libbey writes:

> In July the Commissioner and myself went out in the schooner *Grampus*, south of Martha's Vineyard, to the area which seemed to promise a reward for our labors. We found the temperature conditions right, set the cod trawls, and caught the tilefish. During the remaining portion of the summer I spent considerable time tracing out the limits of the area over which the temperature of 50° and above could be found, using the trawl lines at the same time to ascertain if the fish were there. We found them all the way to the Delaware capes, and were satisfied that, though they were not numerous, they had taken advantage of the changed conditions to occupy the area.

It is thus seen that whereas Professor Verrill in 1882 had given reasons for the disappearance of the fish, and had stated that, "It is probable that in a few years they will occupy these grounds by migrating northward, even if there be not enough left here to replenish their race," and although an indiscriminate search of ten years had failed to find any trace of the lost fish, the results of Professor Libbey's temperature investigations enabled him to show that the physical conditions of the sea bottom were variable, to prove that there was a definite movement of warm water toward the area earlier occupied by the tilefish, and to predict that if this movement continued the tilefish would be found again in its old habitat.

Eight specimens of tilefish were taken by the *Grampus* in 1892, as indicated in the following table:

Date.	Station No.	Depth.	Lat. N.			Long. W.			No. of tilefish.	Weight.
		Fms.	°	′	″	°	′	″		*Lbs.*
Trip 1:										
Aug. 5, 1892 ...	1	75	40	04	00	70	27	00	....	....
Aug. 5, 1892 ...	2	70	40	01	00	70	35	00	....	....
Aug. 6, 1892 ...	3	98	40	02	00	70	38	00	....	....
Aug. 6, 1892 ...	4	74	40	06	30	71	00	00	1	7
Aug. 6, 1892 ...	5	76	40	05	00	71	04	00	....	....
Trip 2:										
Aug. 11, 1892 ...	6	84	40	06	00	71	00	00	....	....
Aug. 13, 1892 ...	7	108	39	57	00	71	32	00	....	....
Aug. 13, 1892 ...	8	91	40	01	00	71	25	00	....	....
Trip 3:										
Aug. 18, 1892 ...	9	78	40	08	00	71	08	00	1	13
Aug. 18, 1892 ...	10	82	40	00	00	71	24	00	....	....
Aug. 19, 1892 ...	11	51	40	05	00	71	23	00	....	....
Aug. 20, 1892 ...	12	78	40	02	00	71	28	00	....	....
Trip 4:										
Sept. 7, 1892 ...	13	84	39	36	00	71	46	30	....	....
Sept. 9, 1892 ...	14	79	39	44	30	71	58	00	....	....
Sept. 10, 1892 ...	15	90	39	34	00	72	06	00	....	....
Sept. 10, 1892 ...	16	58	39	38	00	72	16	00	....	....
Trip 5:										
Sept. 17, 1892 ...	17	58	39	40	00	72	34	30	....	....
Sept. 17, 1892 ...	18	65	39	30	00	72	28	00	....	....
Sept. 17, 1892 ...	19	74	39	26	00	72	22	30	1	(?)
Sept. 18, 1892 ...	20	75	39	20	00	72	27	30	3	(?)
Sept. 18, 1892 ...	21	95	39	28	00	72	11	00	....	....
Trip 6:										
Oct. 3, 1892 ...	22	72	38	09	00	73	55	00	....	....
Oct. 7, 1892 ...	23	67	38	25	00	73	36	00	....	....
Oct. 8, 1892 ...	24	70	38	40	00	72	58	00	2	(?)
Oct. 8, 1892 ...	25	85	38	52	00	72	58	00	....	....
Oct. 9, 1892 ...	26	100	39	07	00	72	45	00	....	....

Two of the stations (4 and 9) at which tilefish were taken are located on the original tilefish ground, at a point that had not been tested by either the *Fish Hawk* or the *Albatross*, although the latter vessel in 1883 dredged within 7 miles of this spot, and in 1886 Captain Collins used trawls still nearer. The other stations at which the fish were found (19, 20, and 24) were considerably farther to the west, a locality that had been examined by the *Albatross* in 1883 and again in 1884. This locality, near the great submarine channel which cuts through the continental shelf from the mouth of the Hudson to the deep water underlying the Gulf Stream, was the seat of continued investigations during the following season.*

The reasons for the movements of the *Grampus* in 1892 and 1893 are stated in a communication from Professor Libbey, bearing date April 3, 1899, in reply to certain questions which I had asked.

"With regard to the capture of the tilefish (in 1892), to the westward of the positions where my observations had been made, I would say that the facts which have been published cover only a small amount of the items which are to be derived from a careful and systematic study of the temperature observations. When in Washington, at the time of the conference with Colonel McDonald, I told him that if the tilefish were of a tropical form he might expect to find the fish that year, provided the conditions I anticipated were fulfilled at one of two points, and I marked the positions on a map in his office—one of them being off the Delaware capes, the other south of Martha's Vineyard—and I gave as my reasons that I felt quite sure that the break or depression in the continental edge, representing the bed of the Hudson River, was of such a character and depth as to prevent the tilefish from crossing it, unless the high temperature had proceeded far enough inland, or in toward the land, to make a connection across the upper part of this depression. If you will examine the charts of the Coast Survey you will find that there is a somewhat remarkable depression on the edge of the continental platform to the southeast of the mouth of the Hudson River. It was my idea that a band of warm waters moving in from the southeast would touch this platform; but as the tilefish apparently was a bottom fish, the migration of the school would stop if the temperature variations did not touch the bottom clear around this depression. If such were the case, the fish would be found off the Delaware capes only; but if the connection had been made the fish would probably be found in both places. * * * * * *

"When we succeeded in finding the fish in the area where my observations had been made, I immediately suggested to Colonel McDonald that we follow up the edge of the continental platform, In 1893 the *Grampus* made five trips in search of the tilefish, set the trawls at 18 stations, and caught 53 fish. Although the trawls were set at 5 places near stations 4 and 9, no fish were taken, so that the greater amount of time was spent near the "Hudson Channel," where on one occasion a single set of the trawl yielded 24 fish.

The record for 1893 is as follows:

Date.	Station No.	Depth.	Lat. N.			Long. W.			No. of tilefish.	Weight.
Trip 1:		*Fms.*	°	′	″	°	′	″		*Lbs.*
July 19, 1893...	27	93	39	58	00	71	19	00	....	....
July 20, 1893...	28	75	39	15	00	72	31	30	....	....
July 20, 1893...	29	86	39	14	00	72	29	00	....	....
July 21, 1893...	30	78	39	23	00	72	24	00	1	4
July 21, 1893...	31	74	39	23	00	72	25	00	2	....
July 21, 1893...	32	71	39	22	00	72	24	30	1	....
Trip 2:										
July 25, 1893...	33	70	39	25	00	72	27	00	1	....
July 27, 1893...	34	74	39	20	00	72	28	00	....	....
July 27, 1893...	35	69	39	25	00	72	19	00	*4	....
Trip 3:										
Aug. 10, 1893...	36	79	39	19	30	72	25	30	1	....
Aug. 11, 1893...	37	73	39	20	00	72	28	45	†24	....
Trip 4:										
Aug. 19, 1893...	38	72	39	23	00	72	32	00	6	....
Aug. 20, 1893...	39	72	39	23	00	72	29	00	7	....
Aug. 22, 1893...	40	75	39	18	21	72	23	00	6	....
Aug. 22, 1893...	41	64	39	19	00	72	34	30	....	....
Trip 5:										
Sept. 21, 1893...	42	68	40	04	00	71	25	00	....	....
Sept. 21, 1893...	43	78	40	07	30	71	14	00	....	....
Sept. 22, 1893...	44	65	40	12	00	71	10	00	....	....
Sept. 22, 1893...	45	80	40	14	30	71	01	00	....	....

*Ovaries of fish fully developed. † Spawn in advanced stage.

During 1894, 1895, and 1896 the *Grampus* and *Fish Hawk* were engaged with other work, and it was the general opinion that, although scattered specimens of the tilefish might be found, they were not sufficiently abundant to warrant continued efforts toward their capture.

On February 8, 1897, the 78-ton schooner *Mabel Kenniston* was overtaken by a gale while on the Georges Bank, and was blown to the westward about 120 miles. The exact location is not definitely known, but it was about 140 miles southwest of No Man's Land, in latitude about 39° 40′ N. and longitude 72° 10′ W. Haddock trawls

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to the westward, as far as the season and the finances of the Commission would permit, in order to verify the facts and see whether the conditions of the theory which I had advanced really seemed to hold good along the southwestern projection of the continental platform. As this conference took place on the *Grampus* and no instructions aside from the verbal understanding between us are in existence, the mere fact that such work was done at that time and under my direction can hardly be explained in any other way.

"With reference to the other question, that in 1893 no tilefish were found near the seventy-first meridian, while a large number were taken near 72° 30′ W., 39° 20′ N., this would tend, in my opinion, to confirm this statement, because the location which you have given would seem to show that, if not a permanent break in this Hudson River depression, at least a temporary break had occurred. Some fish must have gone across this break, because we found the proper temperatures and proper conditions all around the sides of this depression in 1892. The warm water may have withdrawn slightly, so as to interrupt the movement of the school of fish along the bottom after that time.

"The answers to your questions all hang together upon the establishment of that one point, and here I think I have temperature observations enough to warrant me in the statement that while we did find the tilefish over the whole area in 1892, it is quite probable that the general conditions had not become permanent along the edge of the continental platform, but that they were still undergoing a species of oscillation. It is my impression that if we have a series of years, in the near future, with a predominance of northwesterly winds, we will be treated sooner or later to a new disappearance or annihilation of that same body of fish, because you will easily see that if the warm band representing the lower layers of the Gulf Stream is ever withdrawn from the continental edge, it will probably be withdrawn in the manner in which I have indicated, and then the conditions for the disappearance of the fish will be at hand once more."

set in 65 fathoms of water, when brought to the surface, yielded a catch of 30 tilefish, weighing from 6 to 15 pounds apiece. These were landed in Gloucester on February 16, where they were distributed, and those who ate them stated that they were "better than salmon." The captain of the *Mabel Kenniston* thought the catch of tilefish would have been considerably larger had it not been that the dogfish were very abundant and troublesome.

In August, 1898, the *Grampus* was placed at the disposal of the Director of the Biological Laboratory of the United States Fish Commission at Woods Hole, and a small party of naturalists, quite ignorant of the catch that had been made by the *Mabel Kenniston* in 1897, boarded the vessel on August 12, for the purpose of examining the surface fauna in the warmer waters of the Gulf Stream, and to make a trial for the tilefish, although the apparatus for the latter work was crude and unsatisfactory. At noon on the 13th of August a trawl was set in 70 fathoms of water in latitude 40° 11′ N. and longitude 70° 48′ W. After it had been on the bottom not more than an hour, it was drawn, and 8 tilefish were taken; fully a third of the hooks had been torn away from the rotten gangings. The capture of these 8 tilefish was a most welcome surprise to those on board of the boat, because the trawl that had been used was in a miserable condition, and baited with squeteague, which are unsuited for this method of fishing. Moreover, the line rested on the bottom but a comparatively short time. The boat was immediately headed for Woods Hole to obtain the necessary equipment for a more careful survey of the tilefish grounds.

The locality that had been thus examined was about 10 miles to the eastward of the position occupied by the *Grampus* in 1892, where McDonald and Libbey had caught the first fishes since the mortality of 1882. It was, however, a spot that had not been examined by the vessels that had searched for the tilefish during the intervening years.

Commissioner George M. Bowers very willingly provided the necessary apparatus for a more thorough examination of the tilefish ground, and on the 30th of August the *Grampus* left Woods Hole, sailed to Newport, where two barrels of small mackerel were taken on board for bait, and early on the morning of August 31 two trawls were set in 75 fathoms of water in latitude 40° 08′ N., longitude 71° 12′ W. This was a point about 20 miles to the westward of the location at which the fish were found on August 13, but when the trawl was drawn and the dory had returned to the boat, 7 beautiful tilefish were thrown on to the deck of the *Grampus*. With these were two large skates, two squid, and a small hake. Two trawls, each 200 fathoms in length, were used, and each trawl was provided with 300 hooks. The tilefish were all caught on hooks that had been baited with mackerel. The skates were taken on hooks that had been baited with squeteague.

The boat then ran a few miles to the eastward and the trawls, again baited with mackerel, were set in 75 fathoms. After remaining out for a few hours they were hauled, and from the deck of the *Grampus* we could see the sailors tugging at the line and rolling the great fish over into the boat. When the dory came alongside, the men threw 47 beautiful tilefish on the deck. This was the greatest catch since the mortality of 1882, and proved conclusively that the animal was reestablished in its former habitat.

There was time before dark for the trawls to be set again, although they could remain out but a short time; 19 additional fish, however, were taken, making a total of 73 for the entire day. Although many were young fish weighing less than 2 pounds, several were over 20 pounds in weight. The presence of large numbers of young fish is of considerable biological importance, for it indicates that the fish are breeding, and that those now found on the old tilefish ground are not there as a result of migration.

On the following day, September 1, three sets were made, yielding 78 fish, and as the bait was now exhausted, the *Grampus* headed for Montauk Point for the purpose of distributing her fare to the soldiers at Camp Wickoff.

After returning from Camp Wickoff, the *Grampus* was delayed at Woods Hole until the latter part of the month. On September 28 Captain Hahn set sail for the edge of the Gulf Stream, with instructions to find, if possible, the eastern limit of distribution of the tilefish. On September 29 he set two tubs of trawl in latitude 40° 01′ N., longitude 69° 54′ W., in 77 fathoms. The trawls were allowed to remain out 2½ hours, and when hauled 61 tilefish, 1 dogfish, 12 skate, and 3 eels were taken. At 10 a. m. on the same day the lines were set some 8 miles to the eastward, and, after 3 hours, 59 tilefish, 100 dogfish, and 2 skate were captured. At 3 p. m. 3 tubs of trawl were set about 5 miles farther to the eastward, in 72 fathoms of water, and remained out for 2½ hours. While this set was being drawn into the dory unfortunately the line parted, and presumably half the fish were lost. It was dark and the outer buoy could not be located. The fragment of line contained 38 tilefish, and nearly every hook not occupied by a tilefish had caught a dogfish; indeed, the great number and weight of the dogfish accounted for the parting and loss of the line.

On the morning of September 30 a trawl was set in 76 fathoms, latitude 40° 03′ N., longitude 69° 16′ W. It was out 3 hours, and when drawn into the dory 19 tilefish, 2 skate, and 4 hake were taken. At this time only 1½ tubs of trawl were used, about 550 hooks. Still farther to the east, at station 12, only 14 tilefish were taken, and, at the easternmost station, 40° 05′ N., 69° 06′ W., only 12 tilefish were caught, 1½ tubs of trawl line being used.

It would appear from these figures that Captain Hahn had found the eastern boundary of the tilefish "bank," near the sixty-ninth meridian, although even at his last trial several large fish were taken.

This was the last excursion for tilefish made in 1898, and it may be safe to conclude that, inasmuch as on every occasion that the trawl was set in water of appropriate depth the tilefish were found, their area of distribution probably extends from 69° to 73° west longitude, and along a band of the sea bottom of varying width, and from 70 to 80 fathoms in depth, although no tests were made in deeper water.

A tabulated statement of the localities which were examined follows:

Date.	Station No.	Depth.	Lat. N.			Long. W.			No. of tilefish.	Weight.
Trip 1:		*Fms.*	°	′	″	°	′	″		*Lbs.*
Aug. 13, 1898...	1	75	40	11	00	71	48	00	8	....
Trip 2:										
Aug. 31, 1898...	2	75	40	08	00	71	12	45	7	....
Aug. 31, 1898...	3	75	40	12	00	71	05	00	47	350?
Aug. 31, 1898...	4	75	40	11	15	71	03	45	19	74
Sept. 1, 1898...	5	80	40	14	15	71	00	15	24	80?
Sept. 1, 1898...	6	....	40	15	30	70	55	45	39	825?
Sept. 1, 1898...	7	....	40	16	00	70	54	30	15	138
Trip 3:										
Sept. 29, 1898...	8	77	40	01	00	69	54	30	61	658
Sept. 29, 1898...	9	71	40	04	00	69	45	30	59	825
Sept. 29, 1898...	10	72	40	04	00	69	39	00	38	422
Sept. 30, 1898...	11	76	40	03	00	69	16	00	19	214
Sept. 30, 1898...	12	70	40	04	30	69	11	00	14	96
Sept. 30, 1898...	13	75	40	05	30	69	06	00	12	120
Oct. 1, 1898...	14	60	40	10	00	69	50	00	....	....

Measurements of weight and length of fish caught during the excursions of 1898 are recorded here, since they may form a basis for estimating the rate of growth during succeeding years:

Weight and length of tilefish taken in 1898.

Date.	Station No.	Fish No.	Length.	Weight.	Date.	Station No.	Fish No.	Length.	Weight.
			Inches.	*Pounds.*				*Inches.*	*Pounds.*
Aug. 13	1	1	....	....	Aug. 31	4	12	22.50	3.75
Aug. 13	1	2	....	....	Aug. 31	4	13	23.50	5
Aug. 13	1	3	....	....	Aug. 31	4	14	24	4.50
Aug. 13	1	4	....	....	Aug. 31	4	15	24.50	6
Aug. 13	1	5	....	....	Aug. 31	4	16	25.50	5.50
Aug. 13	1	6	....	....	Aug. 31	4	17	29	10.50
Aug. 13	1	7	....	....	Aug. 31	4	18	31	12
Aug. 13	1	8	....	....	Aug. 31	4	19	33	14
Aug. 31	2	1	12.75	....	Sept. 1	5	1	13	.50
Aug. 31	2	2	13	....	Sept. 1	5	2	13	.50
Aug. 31	2	3	13.25	....	Sept. 1	5	3	13.50	.50
Aug. 31	2	4	13.75	....	Sept. 1	5	4	13.50	.50
Aug. 31	2	5	14	....	Sept. 1	5	5	13.50	.50
Aug. 31	2	6	14	....	Sept. 1	5	6	13.75	.50
Aug. 31	2	7	15.75	....	Sept. 1	5	7	13.75	.50
Aug. 31	3	1	17	1.50	Sept. 1	5	8	14	.50
Aug. 31	3	2	17	1.50	Sept. 1	5	9	14	.50
Aug. 31	3	3	17.25	1.75	Sept. 1	5	10	14	.50
Aug. 31	3	4	17.25	1.75	Sept. 1	5	11	14	.50
Aug. 31	3	5	17.50	1.75	Sept. 1	5	12	14	.50
Aug. 31	3	6	17.50	1.50	Sept. 1	5	13	14.50	.75
Aug. 31	3	7	17.50	1.75	Sept. 1	5	14	17.25	1.75
Aug. 31	3	8	17.50	1.50	Sept. 1	5	15	17.50	1.75
Aug. 31	3	9	18	2	Sept. 1	5	16	17.50	1.75
Aug. 31	3	10	18	2	Sept. 1	5	17	17.75	1.375
Aug. 31	3	11	18	2	Sept. 1	5	18	18	1.75
Aug. 31	3	12	18	2	Sept. 1	5	19	18.75	2
Aug. 31	3	13	18	1.75	Sept. 1	5	20	20.75	3.50
Aug. 31	3	14	18	1.50	Sept. 1	5	21	23.75	5.50
Aug. 31	3	15	18	1.75	Sept. 1	5	22	29	11.50
Aug. 31	3	16	18	2	Sept. 1	5	23	29.50	12
Aug. 31	3	17	18.25	2	Sept. 1	5	24	33.50	20
Aug. 31	3	18	22.50	5	Sept. 1	6	1	17	1.50
Aug. 31	3	19	23	5	Sept. 1	6	2	18	1.75
Aug. 31	3	20	23	4.75	Sept. 1	6	3	18	1.75
Aug. 31	3	21	23	5	Sept. 1	6	4	18.25	2
Aug. 31	3	22	23	5	Sept. 1	6	5	18.75	2
Aug. 31	3	23	23	5	Sept. 1	6	6	19	2
Aug. 31	3	24	23	4.50	Sept. 1	6	7	20.75	3
Aug. 31	3	25	23.25	4.50	Sept. 1	6	8	21	2.50
Aug. 31	3	26	23.50	5	Sept. 1	6	9	22.75	5
Aug. 31	3	27	23.50	4.75	Sept. 1	6	10	22.75	5
Aug. 31	3	28	24	5	Sept. 1	6	11	23.25	5.50
Aug. 31	3	29	24	5.50	Sept. 1	6	12	23.50	6.50
Aug. 31	3	30	24	5.50	Sept. 1	6	13	23.50	4.75
Aug. 31	3	31	25	7.50	Sept. 1	6	14	24	5.50
Aug. 31	3	32	25	7	Sept. 1	6	15	24	6
Aug. 31	3	33	26	....	Sept. 1	6	16	24.50	5.50
Aug. 31	3	34	26	7.50	Sept. 1	6	17	24.75	6.50
Aug. 31	3	35	26	7	Sept. 1	6	18	25	8
Aug. 31	3	36	26	8	Sept. 1	6	19	25	6.25
Aug. 31	3	37	28	9.50	Sept. 1	6	20	25	7
Aug. 31	3	38	28	10	Sept. 1	6	21	26	8
Aug. 31	3	39	29	19	Sept. 1	6	22	26	8
Aug. 31	3	40	33	21.50	Sept. 1	6	23	26.50	6.50
Aug. 31	3	41	34	20	Sept. 1	6	24	26.50	8
Aug. 31	3	42	34	19.50	Sept. 1	6	25	26.50	9
Aug. 31	3	43	34	19.50	Sept. 1	6	26	26.50	9
Aug. 31	3	44	34	19	Sept. 1	6	27	28	10
Aug. 31	3	45	34	18	Sept. 1	6	28	28.75	10.50
Aug. 31	3	46	34.50	22	Sept. 1	6	29	29	11
Aug. 31	3	47	34.50	20	Sept. 1	6	30	29	11
Aug. 31	4	1	13.50	.50	Sept. 1	6	31	29.25	11
Aug. 31	4	2	15	.50	Sept. 1	6	32	29.75	12
Aug. 31	4	3	16	.50	Sept. 1	6	33	33	6
Aug. 31	4	4	17.50	1.75	Sept. 1	6	34	33	20
Aug. 31	4	5	18	1.50	Sept. 1	6	35	34	22.50
Aug. 31	4	6	18.50	1.75	Sept. 1	6	36	34	22
Aug. 31	4	7	19	2	Sept. 1	6	37	34	21
Aug. 31	4	8	19	1.375	Sept. 1	6	38	34.50	21
Aug. 31	4	9	19	1.75	Sept. 1	6	39	35	22
Aug. 31	4	10	19.50	1.75	Sept. 1	7	1	17	1.50
Aug. 31	4	11	19.50	1.25	Sept. 1	7	2	17.50	1.75

Weight and length of tilefish taken in 1898—Continued.

Date.	Station No.	Fish No.	Length.	Weight.	Date.	Station No.	Fish No.	Length.	Weight.
			Inches.	*Pounds.*				*Inches.*	*Pounds.*
Sept. 1	7	3	22	4.75	Sept. 29	9	9	26	9
Sept. 1	7	4	22.50	4.50	Sept. 29	9	10	26	11
Sept. 1	7	5	24	6	Sept. 29	9	11	26	10
Sept. 1	7	6	24	5	Sept. 29	9	12	26	9
Sept. 1	7	7	24.50	6.50	Sept. 29	9	13	26	9
Sept. 1	7	8	24.50	7	Sept. 29	9	14	27	10
Sept. 1	7	9	25	7.50	Sept. 29	9	15	27	11
Sept. 1	7	10	25	6	Sept. 29	9	16	27	10
Sept. 1	7	11	28	9.75	Sept. 29	9	17	27	10
Sept. 1	7	12	28.50	10.50	Sept. 29	9	18	27	9
Sept. 1	7	13	31.50	15	Sept. 29	9	19	27	9
Sept. 1	7	14	33	19	Sept. 29	9	20	27	12
Sept. 1	7	15	33.50	20	Sept. 29	9	21	27	9
Sept. 29	8	1	13	1	Sept. 29	9	22	27	11
Sept. 29	8	2	13	1	Sept. 29	9	23	27	11
Sept. 29	8	3	13	1	Sept. 29	9	24	27	10
Sept. 29	8	4	14	9	Sept. 29	9	25	27	9
Sept. 29	8	5	14	1	Sept. 29	9	26	28	11
Sept. 29	8	6	17	24	Sept. 29	9	27	28	12
Sept. 29	8	7	17	2	Sept. 29	9	28	28	10
Sept. 29	8	8	17	2	Sept. 29	9	29	28	10
Sept. 29	8	9	17	2	Sept. 29	9	30	29	9
Sept. 29	8	10	18	2	Sept. 29	9	31	29	10
Sept. 29	8	11	20	9	Sept. 29	9	32	29	9
Sept. 29	8	12	21	3	Sept. 29	9	33	29	10
Sept. 29	8	13	22	5	Sept. 29	9	34	30	12
Sept. 29	8	14	23	1	Sept. 29	9	35	30	9
Sept. 29	8	15	24	27	Sept. 29	9	36	30	12
Sept. 29	8	16	24	10	Sept. 29	9	37	30	10
Sept. 29	8	17	24	8	Sept. 29	9	38	30	12
Sept. 29	8	18	25	7	Sept. 29	9	39	30	11
Sept. 29	8	19	26	10	Sept. 29	9	40	30	10
Sept. 29	8	20	26	8	Sept. 29	9	41	30	11
Sept. 29	8	21	26	10	Sept. 29	9	42	31	10
Sept. 29	8	22	26	9	Sept. 29	9	43	31	23
Sept. 29	8	23	26	11	Sept. 29	9	44	31	11
Sept. 29	8	24	26	9	Sept. 29	9	45	33	20
Sept. 29	8	25	26	6	Sept. 29	9	46	33	20
Sept. 29	8	26	26	11	Sept. 29	9	47	33	22
Sept. 29	8	27	26	10	Sept. 29	9	48	35	21
Sept. 29	8	28	26	10	Sept. 29	9	49	35	22
Sept. 29	8	29	27	5	Sept. 29	9	50	36	21
Sept. 29	8	30	27	11	Sept. 29	9	51	36	23
Sept. 29	8	31	27	7	Sept. 29	9	52	36	24
Sept. 29	8	32	27	20	Sept. 29	9	53	36	27
Sept. 29	8	33	27	16	Sept. 29	9	54	36	22
Sept. 29	8	34	27	10	Sept. 29	9	55	36	26
Sept. 29	8	35	27	11	Sept. 29	9	56	38	24
Sept. 29	8	36	27	9	Sept. 29	9	57	38	27
Sept. 29	8	37	27	11	Sept. 29	9	58	39	29
Sept. 29	8	38	28	12	Sept. 29	9	59	40	26
Sept. 29	8	39	28	10	Sept. 29	10	1	15	1
Sept. 29	8	40	28	2	Sept. 29	10	2	16	1
Sept. 29	8	41	28	11	Sept. 29	10	3	19	3
Sept. 29	8	42	28	13	Sept. 29	10	4	20	2
Sept. 29	8	43	28	13	Sept. 29	10	5	21	8
Sept. 29	8	44	28	13	Sept. 29	10	6	23	6
Sept. 29	8	45	29	11	Sept. 29	10	7	23	6
Sept. 29	8	46	30	10	Sept. 29	10	8	24	10
Sept. 29	8	47	30	15	Sept. 29	10	9	24	10
Sept. 29	8	48	30	16	Sept. 29	10	10	25	8
Sept. 29	8	49	30	15	Sept. 29	10	11	26	9
Sept. 29	8	50	31	4	Sept. 29	10	12	26	11
Sept. 29	8	51	31	15	Sept. 29	10	13	27	9
Sept. 29	8	52	32	19	Sept. 29	10	14	27	9
Sept. 29	8	53	32	21	Sept. 29	10	15	27	10
Sept. 29	8	54	33	18	Sept. 29	10	16	27	10
Sept. 29	8	55	33	9	Sept. 29	10	17	27	9
Sept. 29	8	56	33	10	Sept. 29	10	18	27	10
Sept. 29	8	57	33	25	Sept. 29	10	19	27	10
Sept. 29	8	58	34	15	Sept. 29	10	20	27	11
Sept. 29	8	59	35	26	Sept. 29	10	21	27	9
Sept. 29	8	60	35	24	Sept. 29	10	22	27	10
Sept. 29	8	61	36	22	Sept. 29	10	23	28	10
Sept. 29	9	1	10	26	Sept. 29	10	24	28	11
Sept. 29	9	2	24	9	Sept. 29	10	25	28	11
Sept. 29	9	3	24	9	Sept. 29	10	26	29	11
Sept. 29	9	4	25	9	Sept. 29	10	27	29	12
Sept. 29	9	5	25	9	Sept. 29	10	28	29	13
Sept. 29	9	6	26	10	Sept. 29	10	29	30	14
Sept. 29	9	7	26	9	Sept. 29	10	30	30	14
Sept. 29	9	8	26	9	Sept. 29	10	31	31	15

Weight and length of tilefish taken in 1898—Continued.

Date.	Station No.	Fish No.	Length.	Weight.	Date.	Station No.	Fish No.	Length.	Weight.
			Inches.	*Pounds.*				*Inches.*	*Pounds.*
Sept. 29	10	32	31	16	Sept. 30	12	1	15	2
Sept. 29	10	33	33	16	Sept. 30	12	2	18	2
Sept. 29	10	34	33	19	Sept. 30	12	3	18	2
Sept. 29	10	35	34	19	Sept. 30	12	4	18	2
Sept. 29	10	36	34	24	Sept. 30	12	5	18	2
Sept. 29	10	37	35	22	Sept. 30	12	6	21	5
Sept. 29	10	38	36	23	Sept. 30	12	7	25	7
Sept. 30	11	1	16	2	Sept. 30	12	8	26	12
Sept. 30	11	2	18	2	Sept. 30	12	9	26	9
Sept. 30	11	3	24	12	Sept. 30	12	10	27	9
Sept. 30	11	4	24	6	Sept. 30	12	11	28	10
Sept. 30	11	5	27	10	Sept. 30	12	12	28	10
Sept. 30	11	6	27	11	Sept. 30	12	13	29	11
Sept. 30	11	7	27	9	Sept. 30	12	14	30	13
Sept. 30	11	8	27	9	Sept. 30	13	1	13	1
Sept. 30	11	9	27	8	Sept. 30	13	2	14	1
Sept. 30	11	10	27	9	Sept. 30	13	3	16	2
Sept. 30	11	11	27	10	Sept. 30	13	4	18	2
Sept. 30	11	12	27	12	Sept. 30	13	5	27	10
Sept. 30	11	13	27	11	Sept. 30	13	6	27	11
Sept. 30	11	14	28	10	Sept. 30	13	7	29	12
Sept. 30	11	15	29	11	Sept. 30	13	8	29	13
Sept. 30	11	16	30	13	Sept. 30	13	9	30	13
Sept. 30	11	17	36	26	Sept. 30	13	10	30	13
Sept. 30	11	18	36	19	Sept. 30	13	11	30	15
Sept. 30	11	19	36	24	Sept. 30	13	12	36	27

Following are abstracts of some recent letters concerning the food qualities of the tilefish:

[From Mr. H. R. Storer, Providence, R. I.]

The tilefish was boiled for dinner, and what was left therefrom warmed with cream for breakfast the next morning. Both dishes proved delicious, even more so than cod, which is my favorite. I sent a portion of the fish to my neighbor, Mr. Benj. R. Smith, and his family gave an equally satisfactory report.

[From Mr. W. P. Titcomb, Washington, D. C.]

Regarding the sample of the tilefish with which you favored me last week, I have to say that I rate it as equal in texture and flavor to any salt-water fish, except the mackerel, which of course will not bear transportation and retain its flavor as the tilefish evidently does. Although very fond of halibut, and rating it very highly, I am inclined to think from this, the only sample of tilefish which I have tasted, that I should regard it as equally desirable.

[From Mr. Lucian D. Sharpe, II, Providence, R. I.]

I wish to acknowledge the fine tilefish you were kind enough to send us. We enjoyed it very much, and the flesh was quite fine and sweet, though with not as much flavor as some fish have.

[From Mr. Nathan Babcock, Westerly, R. I.]

Through the kindness of Mr. J. A. Ripple I had a sample of the "tile," the rediscovered fish. I think it is an excellent fish. It far surpasses the cod. It is delicate in flavor, and in all respects very palatable. It will find favor with those who enjoy good fish.

[From Mr. J. M. K. Southwick, Newport, R. I.]

I promised you a report on the tilefish. Briggs thinks it rather dry and tasteless. H. Christian thought it very good. Charles Clark baked his and liked it very much. J. I. Wright boiled his and says it was excellent; knew no fish he liked better; thought it very good, better than cod. Edw. Lilley thought it very nice. Capt. J. V. Cotton says it was between a cod and a halibut. The writer boiled his and remarked the same lack of taste noted by Briggs, but juicy, not dry. I consider it a very valuable edible fish.

[From Mr. John F. Calkins, Providence, R. I.]

Tilefish is good. Boiled, first class; broiled, fair; made into a salad, excellent. I think that with proper preparation it would be good baked. Of course, like all fish, the fresher the better. I see no reason why it should not become a valuable addition to our list of food-fishes. It should not be boiled one moment beyond the point of "done." I noted plenty of gelatine in it.

[From Messrs. Johnson & Smith, Boston, Mass.]

Yours in regard to the tilefish received, asking our opinion of it. We found it to be a good fish for eating, having a fine flavor, resembling that of our striped bass or what they call in Washington rockfish. It has also lasting qualities, remaining in good condition for several days, which is greatly in its favor. We hope that we may soon have more of it.

[From Hon. Eugene G. Blackford, New York, N. Y.]

In reply to your favor of the 20th, permit me to say that I consider the tile an excellent table fish. The flesh is somewhat coarse, but very sweet, and I should say that it more nearly resembles the blackfish or tautog than any other fish I can recall. I should recommend to those testing its edible qualities to have it baked and served with a brown sauce.

Out of the fish that you sent as an experiment to this market I selected some for a dinner at the Union Club of this city—the most prominent of all our clubs. The fish was served to about twenty-five gentlemen, nearly all of whom might be considered gastronomical experts, and they were all delighted with it. I may say parenthetically that the fish were at least a week old when they were served, so that I question whether the best possible results were obtained from the test of their edible qualities.

ON THE MOVEMENTS OF CERTAIN LOBSTERS LIBERATED AT WOODS HOLL.

By H. C. BUMPUS.

U. S. Fish Commission Bulletin for 1899.

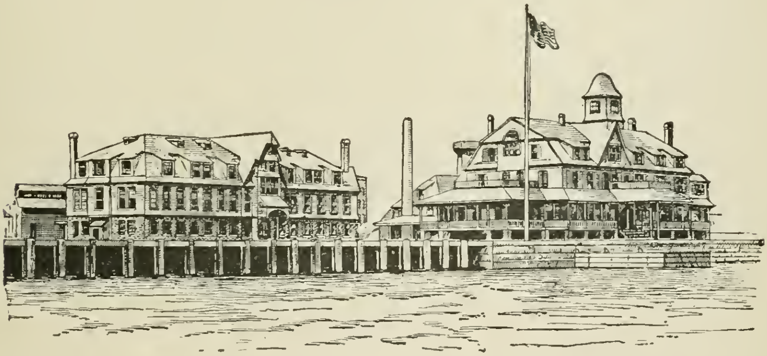
U. S. COMMISSION OF FISH AND FISHERIES,
GEORGE M. BOWERS, Commissioner.

CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION, WOODS HOLE, MASSACHUSETTS.

ON THE
MOVEMENTS OF CERTAIN LOBSTERS LIBERATED AT WOODS HOLE.

BY

HERMON C. BUMPUS, Ph. D.,
Director of Biological Laboratory of United States Fish Commission at Woods Hole.



Extracted from U. S. Fish Commission Bulletin for 1899. Pages 225 to 230. Plate 27.

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Contributions from the Biological Laboratory of the U. S. Fish Commission, Woods Hole Massachusetts.

ON THE MOVEMENTS OF CERTAIN LOBSTERS LIBERATED AT WOODS HOLE DURING THE SUMMER OF 1898.

By HERMON C. BUMPUS,
Director of Biological Laboratory of the U. S. Fish Commission at Woods Hole.

For several years, during the spring and early summer, a large number of egg-bearing lobsters have been collected from the shores of Connecticut, Rhode Island, and southern Massachusetts and brought to the hatchery at Woods Hole, where the eggs have been removed and the "stripped" animals returned to the ocean, either at Woods Hole or, in special cases, near the place of capture. The lobsters were of good size, generally exceeding 10½ inches in length, although some were smaller, especially those from the shores of Rhode Island, where the marketable length is only 9½ inches.

It occurred to the writer that data respecting the movements and habits of female lobsters at the close of the breeding season might be secured if the animals should be tagged before liberation, and accordingly copper tags, bearing consecutive numbers and the request that they be returned to the Commission, were attached to the rostrums of about 500 specimens, and these animals were liberated during June and July, 1898. On the 17th of June 34 lobsters, numbered 582 to 615 inclusive, were "stripped," tagged, and liberated in Vineyard Sound, near Lackey Bay. Six of these were subsequently captured by lobster fishermen and the tags were returned to the Commission.

This group of lobsters yielded data as follows:

No.	Liberated.		Recaptured.		No. of days free.	Distance (miles).	Direction.
	Locality.	Date.	Locality.	Date.			
594	Lackey Bay	June 17	Menemsha	(?)	(?)	9	SSW.
595	do	do	Vineyard Sound	July 11	24	0	0
604	do	do	do	June 17	1	0	0
606	do	do	do	July 5	18	0	0
609	do	do	do	July 11	24	0	0
611	do	do	Menemsha	(?)	(?)	9	SSW.

The four recaptured near the place of liberation were taken by Mr. Alfred Nickerson, whose traps are near the southerly opening of Woods Hole, extending from Nobsque to Lackey Bay. The distance traveled by these lobsters can, therefore, only be estimated, although the most remote traps were probably not more than a mile or two from the point of liberation. One was captured on the day of its liberation. Mr. Hillman, whose traps were located near Gayhead, returned tags 594 and 611 to the Commission, but unfortunately he did not return dates with his tags, so that the rate of travel of these and other lobsters taken by him can not be given. It will be noted that the general course of the lobsters is toward the south and west.

On the 18th of June 94 lobsters were tagged and placed on the steamer that runs from Woods Hole to New Bedford. The writer deposited 33 of these in Buzzards Bay, near the westerly opening of Woods Hole; 17 when the steamer was about midway between Woods Hole and New Bedford; 33 at a point south of West Island, and 11 as the steamer passed Black Rock. For convenience these stations have been named A, B, C, and D, respectively, and are so indicated on the chart at the end of this paper. Along this course of the steamer there is an almost continuous series of lobster pots extending entirely across the bay, many of them owned by Greeks and Portuguese, who are somewhat disinclined to return the tags, preferring to keep them as charms. It is perfectly safe, therefore, to conclude that only a small proportion of the tags taken are finally returned to the Commission.

From station A, 4 tags were recovered; from station B, none; from station C, 4, and from station D, 2. The details are as follows:

No.	Liberated.		Recaptured.		No. of days free.	Distance (miles).	Direction.
	Locality.	Date.	Locality.	Date.			
618	Station A	June 18	Near Hen and Chickens	July 15	27	16	WSW.
628	do	do	Cuttyhunk	July 30	42	12	WSW.
629	do	do	Near West Island	July 9	21	4	WNW.
645	do	do	do	July 2	14	4	WNW.
650	Station C	do	Cuttyhunk	July 1	13	9	SW.
654	do	do	Near Station A	June 29	11	4	E.
667	do	do	Penikese	July 7	19	6	SW.
681	do	do	Near Station C	June 30	12	0	0
699	Station D	do	Near Station D	July 9	21	0	0
705	do	do	do	June 30	12	0	0

None of the lobsters distributed on June 18 took a northerly course, and although three were taken at points roughly described as east of their place of liberation, four traveled toward the mouth of the bay, all of them considerable distances, and No. 618 made a journey of 16 miles between June 18 and July 15, twenty-seven days. This is the longest distance traveled by any of the lobsters. Those liberated at stations B, C, and D were taken originally at Cuttyhunk. The fact that two of these, Nos. 650 and 667, returned to their former place of capture may indicate a strong homing instinct.

On the 24th of June 62 lobsters, originally from Noank, Stonington, and Block Island, were liberated at Quicks Hole at a point indicated on the chart. The tags of eight of these were returned to the Commission. The details are as follows:

No.	Liberated.		Recaptured.		No. of days free.	Distance (miles).	Direction.
	Locality.	Date.	Locality.	Date.			
711	Quicks Hole	June 24	Quicks Hole	July 5	11	0	0
714	do	do	do	June 28	4	0	0
715	do	do	Menemsha	(?)	(?)	5	SSE.
730	do	do	Robinsons Hole	June 30	6	2	E.
743	do	do	Quicks Hole	July 8	14		
747	do	do	Menemsha	(?)	(?)	5	SE.
756	do	do	Cuttyhunk	July 19	25	6	WSW.
759	do	do	Robinsons Hole	July 5	11	2	E.

Of the animals liberated on June 24, it might be said that their course was not so characteristically toward the south as were the courses taken from some of the other stations, but the three which had traveled a sufficient distance from the point of liberation to give a distinct trend to their course did move in the same direction as those of other stations. As the lobster pots are not set in large numbers off shore, lobsters liberated at Quicks Hole naturally would not stand the same chance of recapture toward the south and west that they would toward the north and east, and therefore it would seem to be of more than passing interest that from this southern point of distribution no lobsters were found to migrate to any considerable distance either up the sound toward Woods Hole or across the bay toward New Bedford.

A second lot, of 140 lobsters, was liberated off Nobsque on the same day as those liberated at Quicks Hole. These were quite at liberty to migrate in a northeasterly direction, but all reports of their capture came from the southwest. That so many of these and other lobsters took a southwesterly course would seem to prove that there is in general a decidedly southerly and westerly trend to their migrations, although I am not prepared to say whether this is in response to a strong homing impulse, or an effort to pass from warmer into colder water, or from shallow into deeper water. The proportion of animals captured to those liberated is noteworthy. Of 140 liberated at Nobsque, tags were received from 29. The details are as follows:

No.	Liberated.		Recaptured.		No. of days free.	Distance (miles).	Direction.
	Locality.	Date.	Locality.	Date.			
779	Nobsque	June 24	Woods Hole	July 11	17	0	0
789	do	do	Nobsque	July 5	11	0	0
791	do	do	do	July 11	17	0	0
798	do	do	Cedar Tree Neck	Sept. 21	89	5	SSW.
800	do	do	Woods Hole	July 11	17	0	0
802	do	do	Tarpaulin Cove	July 8	14	5	WSW.
807	do	do	Vineyard Sound	Aug. 11	48	2	SE.
819	do	do	Woods Hole	Aug. 28	65	0	0
821	do	do	Tarpaulin Cove	July 18–23	26	4	WSW.
825	do	do	Menemsha	?	?	11	SSW.
828	do	do	Nobsque	July 11	17	0	0
830	do	do	Tarpaulin Cove	July 18–23	26	4	WSW.
831	do	do	Vineyard Sound	do	26	4	WSW.
834	do	do	Menemsha	?	?	10	SSW.
838	do	do	Neshewena	July 8	14	12	WSW.
848	do	do	Gay Head	Aug. 15	52	13	SW.
851	do	do	Vineyard Haven	July 5	11	4	SE.
868	do	do	Quicks Hole	do	11	11	WSW.
869	do	do	Tarpaulin Cove	July 18–23	26	5	WSW.
872	do	do	Vineyard Haven	do	26	5	WSW.
879	do	do	Nobsque	?	?	0	0
883	do	do	Robinson Hole	July 20	26	8	WSW.
889	do	do	Quicks Hole	July 23	29	9	WSW.
891	do	do	Nobsque	?	?	0	0
896	do	do	Vineyard Sound	?	?	6	WSW.
901	do	do	Menemsha	?	?	11	SSW.
902	do	do	Nobsque	July 11	17	0	0
904	do	do	Menemsha	?	?	9	SSW.
907	do	do	do	?	?	11	SSW.

On the 25th of June 58 lobsters were liberated near the can buoy at the entrance of Woods Hole Harbor. Of these, only three were recaptured. No. 928 remained in the neighborhood until September 15, when it was captured near the Wepeckets. The capture of this and other specimens would go to show that molting does not always take place immediately after the eggs have reached maturity, for, if the animals had molted, the tags would have been lost.

No.	Liberated.		Recaptured.		No. of days free.	Distance (miles).	Direction.
	Locality.	Date.	Locality.	Date.			
928	Can buoy	June 25	Wepeckets	Sept. 15	82	3	WNW.
945	do	do	Woods Hole	July 23	28	0	0
960	do	do	Quicks Hole	do	28	9	WSW.

On July 2 two lots of lobsters were liberated, 60 at Lackey Bay and 49 at Woods Hole. Of the former, 5 were recaptured, as follows:

No.	Liberated.		Recaptured.		No. of days free.	Distance (miles).	Direction.
	Locality.	Date.	Locality.	Date.			
980	Lackey Bay.	July 2	Vineyard Sound	July 11	9	0	0
999	.....do	.....do	.....do	July 20	18	0	0
1020	.....do	.....do	Quicks Hole	July 23	21	6	WSW.
1034	.....do	.....do	Wepeckets	July 7	5	2	NW.
1098	.....do	.....do	Robinson Hole	July 20	18	8	WSW.

It will be noted from the above that the trend of migration of all those that had traveled a considerable distance after liberation was in the same general direction as that taken by those liberated from the stations mentioned.

The lobsters in the second lot liberated on July 2 were thrown into the water near the Fish Commission station, and not only is the direction of their course interesting, but the rate of movement of certain individuals is far beyond one's expectation. The animals traveled down the bay in a west southwesterly direction at a rate that seemed to indicate their desire to place as much distance as possible between themselves and the hatchery. No. 1000 made the journey from Woods Hole to Cuttyhunk in 3 days, No. 1022 reached the neighborhood of the Hen and Chickens lightship in 6 days, and No. 1014 reached an equally remote point in 7 days. The following table will give additional data relative to the movements of this last series:

No.	Liberated.		Recaptured.		No. of days free.	Distance (miles).	Direction.
	Locality.	Date.	Locality.	Date.			
970	F. C. Station	July 2	Cuttyhunk	July 16	14	14	WSW.
971	.....do	.....do	.....do	July 13	11	14	WSW.
977	.....do	.....do	.....do	July 16	14	15	WSW.
991	.....do	.....do	Woods Hole	July 7	5	0	....
1000	.....do	.....do	Cuttyhunk	July 5	3	12	WSW.
1006	.....do	.....do	Wepeckets	Sept. 15	75	3	WSW.
1009	.....do	.....do	Woods Hole	July 11	9	0	....
1010	.....do	.....do	Cuttyhunk	July 13	11	12	WSW.
1013	.....do	.....do	Woods Hole	July 7	5	0	....
1014	.....do	.....do	Hen and Chickens	July 9	7	15	WSW.
1019	.....do	.....do	Wepeckets	Sept. 15	75	3	W.
1022	.....do	.....do	Hen and Chickens	July 8	6	15	WSW.
1030	.....do	.....do	Wepeckets	Sept. 15	75	4	WSW.
1054	.....do	.....do	.....do	.....do	75	3	W.
1055	.....do	.....do	Penikese	July 26	24	11	WSW.

Attention has already been called to the strong migratory impulse which controlled the movements of the animals set at liberty, and it must be left for subsequent observations to determine the reason therefor. During the latter part of June and the early part of July the water near Woods Hole ranges in temperature from 62° to 69° F., and as the water in this portion of the bay and sound is received from the presumably cooler water of the southwest, the inclination of the liberated animals to seek cooler water may account for the uniformity in their movements. But lobsters are caught about the station during the entire summer, and the uniformly small size of these animals would indicate that they remain in the locality during the season and are not caught as they pass through the sound on their migrations.

It has been already suggested that the uniformity in the movements of the tagged lobsters may be the result of a homing instinct. This question might be answered in the following way: If lobsters caught at Woods Hole and released at Gay Head were recaptured at Woods Hole, and if lobsters taken at the same time at Gay Head and released at Woods Hole were recaptured at Gay Head, it would seem that only a homing instinct could account for the movement.

It is quite possible that during June and July lobsters seek deeper water, although it is generally believed that during the spring and early summer the general migration is from deeper to more shallow water, and that the return to the deeper water does not occur until fall. During the summer months lobsters are caught off the coast of Maine in shallow water, ranging from 3 to 10 fathoms in depth, and it is not until October and November that the pots are set in deeper water, from 35 to 40 fathoms. Professor Herrick states that the fishermen generally take their traps from the deeper water and place them in the shallow water of the sound at about the time that we have found the animals seeking the deeper water. From the neighborhood of Gay Head the general migration into deeper water is said to begin the latter part of August and to continue during September and October. If a relatively large number of both sexes, and of different sizes, should be captured at Cuttyhunk or a place similarly located, and after being tagged should be returned to the place of their capture, valuable data of a positive nature would undoubtedly be secured. One wishes that this might be attempted.

It is possible that the movements are not dependent upon any of the above-mentioned factors, but that the supply of food is all-controlling. The peculiar behavior of female lobsters in the vicinity of No Mans Land, as observed by Mr. Vinal Edwards and recorded by Professor Herrick, would seem, however, to make this improbable.

In writing of the lobster's powers of movement, Professor Herrick says that by the flexion of its abdomen the animal is able to shoot backward through the water with astonishing rapidity, sometimes going, according to one observer, 25 feet in less than a second. He quotes Travis as follows:

> In the water they can run nimbly upon their legs or small claws, and, if alarmed, can spring tail forward to a surprising distance, as swift as a bird can fly. The fishermen see them pass about 30 feet, and by the swiftness of their motion suppose that they go much farther. Athenæus remarks this circumstance, and says that incurved lobsters will spring with the activity of dolphins.

While we do not know what method of progression lobster No. 1000 adopted in making her record of 12 miles in 3 days, we do know from the course taken by this animal, as well as by Nos. 1014 and 1022, that associated with their rapidity of movement there is remarkable endurance.

It is generally believed that the female lobster molts very soon after its young have escaped from the egg membranes, and although it is manifestly incorrect to consider a lobster artificially freed from its eggs as one which has completed the incubation period, the fact that many were recaptured with tags long after the period at which the young would probably have hatched under normal conditions, is a proof that in many cases females do not change their covering as soon as they are relieved of the obligations of maternity. One tag was taken as late as September 21.

One of the most interesting results from this series of experiments is the direct evidence of the merciless persecution of the lobster. The chances of continued life for a lobster that has reached a marketable size are extremely slight. Of the 140 liberated at Nobsque, more than 20 per cent are known to have been captured within three months, and 15 of the 49 liberated on July 2 at Woods Hole, or fully 30 per cent, were taken by September 15. Of course, these numbers do not begin to show

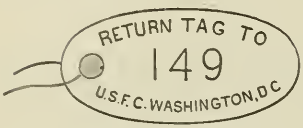
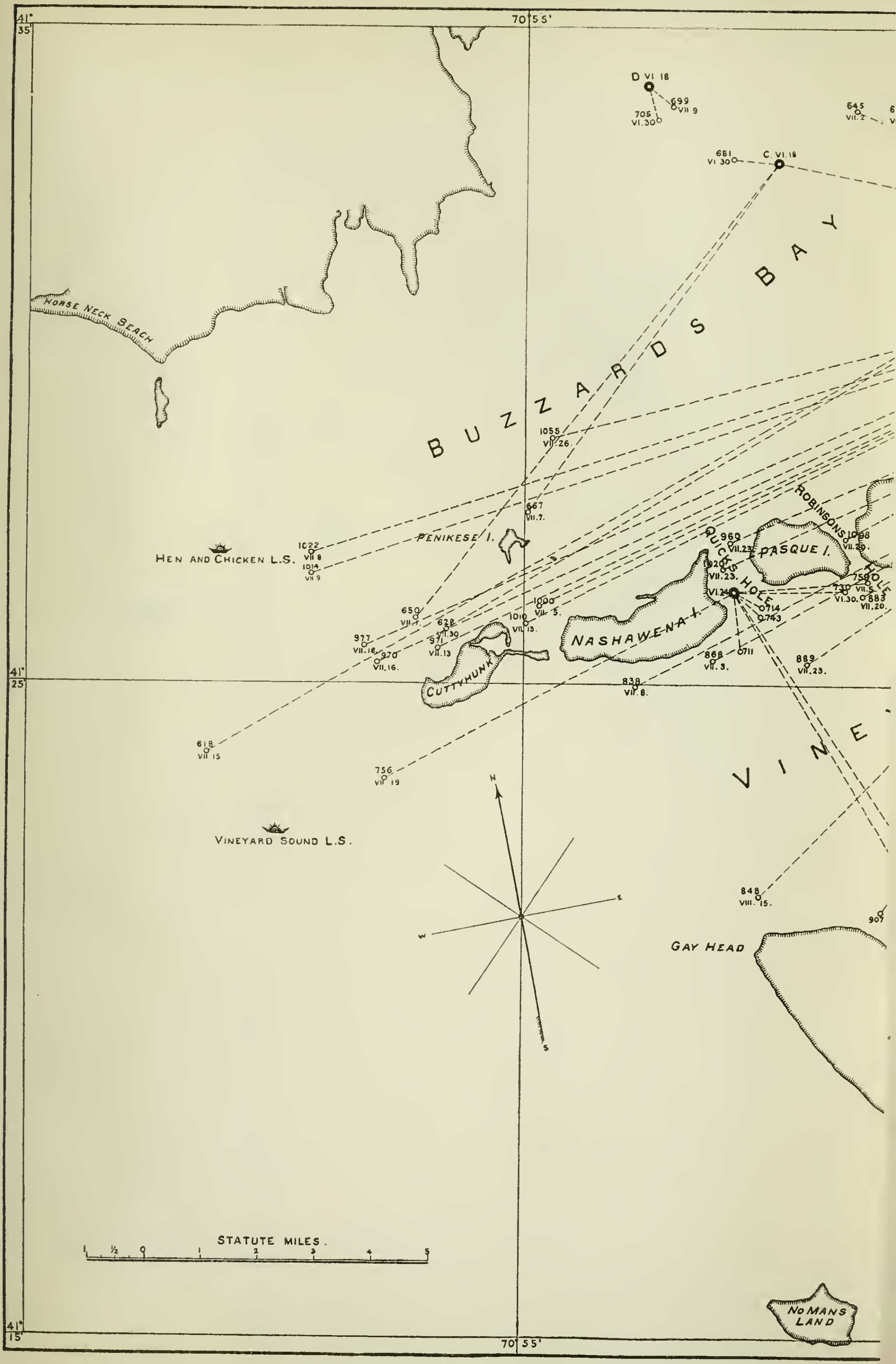


Figure of tag—exact size.

what actually occurs, for many fishermen are known not to have returned the tags; a large number of tags are doubtless lost by the process of molting, and not a few of the animals perish from rough treatment received during captivity. It should be remembered that when first captured they are thrown from the pot into the boat, and from the boat into a car, where they may remain several days awaiting the arrival of a smack to convey them to the station. While in the car they suffer from their own belligerency, and when thrown into the well of the smack and during their journey to Woods Hole not a few perish. Moreover, at the station they are handled several times before they are finally stripped, tagged, recorded, and made ready for their liberation.

But without attempting to make any estimate of the number that reached the market without leaving a completed record, and confining ourselves to the data derived from those that were recaptured, we find that of a total of 479 lobsters liberated, 76 very soon found their way to market. It is therefore evident that, unless the supply of any one locality is replenished, either by immigration or by artificial propagation, the lobster will be exterminated; indeed elimination has actually occurred at certain localities, and there is every indication that before long an industry which has yielded many millions of dollars will have perished through the inexcusable abuses of our fishing privileges.

BROWN UNIVERSITY,
Providence, Rhode Island.


41° 35'
70° 55'
D VI 18
699 VII 9
705 VI.30
645 VII.2
681 VI 30
C. VI.18
BUZZARDS BAY
HORSE NECK BEACH
1055 VII.26.
667 VII.7.
HEN AND CHICKEN L.S.
1022 VII 8
1014 VII 9
PENIKESE I.
ROBINSONS HOLE
960 VII.23
PASQUE I.
1098 VII.29.
QUICKS HOLE
1020 VII.23.
VI.24
758 VII.5
730 VI.30.
883 VII.20.
714
743
711
NASHAWENA I.
1000 VII. 5.
1010 VII.13.
650 VII.7.
628 VII.30
971 VII.13
977 VII.16.
970 VII.16.
CUTTYHUNK
868 VII. 3.
838 VII. 8.
889 VII.23.
41° 25'
618 VII 15
756 VII 19
VINE
N
E
W
S
VINEYARD SOUND L.S.
848 VIII. 15.
907
GAY HEAD
STATUTE MILES.
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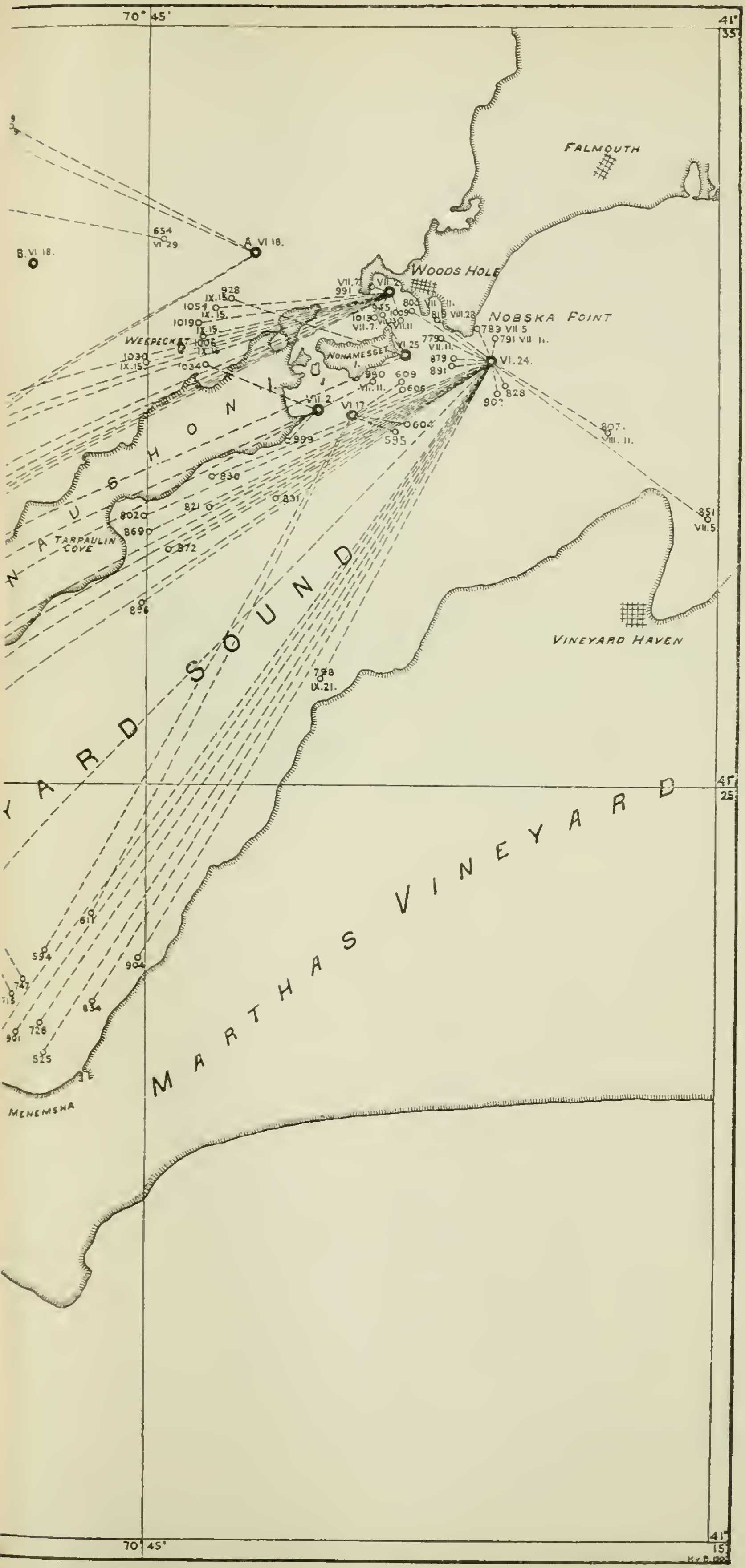
NO MANS LAND
41° 15'
70° 55'


70° 45'
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FALMOUTH
WOODS HOLE
NOBSKA POINT
A VI 18.
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654
VI 29
928
IX.15
1054
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1019
IX.15
WEEPECKET
1006
IX.15
1030
IX.15
1034
VII.7
991
VII.2
945
1013
VII.7.
VII.11
1009
806
VII 11.
819
VIII.28
783 VII 5
791 VII 11.
779
VII.11.
VI.25
NONAMESSET I.
879
891
VI.24.
980
VII.11.
609
606
828
902
807.
VIII. 11.
VII 2
VI 17
604
595
999
NAUSHON I.
836
831
821
802
869
TARPAULIN COVE
872
896
851
VII.5.
VINEYARD HAVEN
VINEYARD SOUND
798
IX.21.
41° 25'
MARTHAS VINEYARD
617
594
742
715
904
834
728
901
525
MENEMSHA
41° 15'
70° 45'

IMPROVEMENTS IN PREPARING FISH FOR SHIPMENT.

By R. W. TOWER.

U. S. Fish Commission Bulletin for 1899.

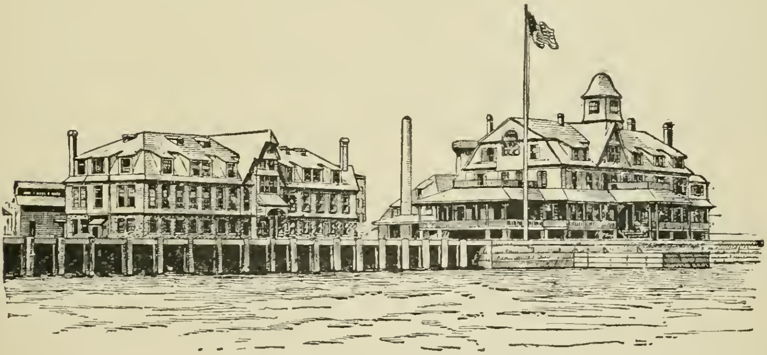
U. S. COMMISSION OF FISH AND FISHERIES,
GEORGE M. BOWERS, Commissioner.

CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION, WOODS HOLE, MASSACHUSETTS.

IMPROVEMENTS IN PREPARING FISH FOR SHIPMENT.

BY

RALPH W. TOWER,
Assistant Professor of Chemical Physiology, Brown University.



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Contributions from the Biological Laboratory of the U. S. Fish Commission,
Woods Hole, Massachusetts.

IMPROVEMENTS IN PREPARING FISH FOR SHIPMENT.

By RALPH W. TOWER,
Assistant Professor of Chemical Physiology, Brown University.

It is well known that ice, as ordinarily used in packing, is more or less unsatisfactory. It spoils the freshness, flavor, and firmness of the fish; but, moreover, the moisture of the melting ice favors the development of putrefactive bacteria and thus hastens decay, which is only the result of the activity of certain putrefactive bacteria. If the fish are so handled that the activity of the bacteria is restricted, the process of decay will be retarded; but if the fish are handled so as to encourage the ravages of the bacteria, the process of decay will progress much more rapidly. The pressing of fish by close packing softens the muscles and renders the flesh more susceptible to invasion by putrefactive bacteria. Packing fish in foul barrels and unclean boxes, the contamination from which is conveyed to the fish by the melting ice, also contributes to their speedy decay.

The following investigations, which were carried on at the biological laboratory of the United States Fish Commission at Woods Hole, were undertaken for the purpose of ascertaining to what degree fish are spoiled by carelessness, filth, and bad packing, and to devise methods which might mitigate these evils.

The animals used for the experiments were squeteague, bonito, blue-fish, and tile-fish. The fish from the large trap owned by the United States Fish Commission and located in Buzzards Bay furnished an unlimited supply of material. During July and August squeteague were abundant; their flesh is soft, very susceptible to invasion by putrefactive bacteria, and difficult to preserve by the ordinary methods of packing. Bonito were also occasionally taken; their flesh is firm and hard and relalatively easy to preserve.

The first experiments were to determine the influence of ordinary summer temperatures and of the different methods of killing and handling upon putrefaction; 48 squeteague were hung up by a wire passing through the eyes; 24 had the intestines removed, after which the fish were immediately drained; the other 24 were not opened. The experiment was made in a place protected from the sun, but to which the air had free access. The weather was humid and foggy, the temperature being 68° at 8 a. m., 72° at noon, and 71° at 5 p. m. After 24 hours the fish were examined. Those that had not been opened were putrid and emitted an almost unbearable odor. Those whose intestines had been removed were in better condition, and might even have been used for food. The abdominal cavity was much fresher and putrefaction had not penetrated so deeply into the flesh. The experiment shows that when the intestines are not removed decomposition takes place more rapidly, and that the immediate removal of the viscera delays decomposition. The experiment gives some idea of the rates of putrefactive changes in the two kinds of fish.

The next experiment was with 24 squeteague and 6 bonitos. After removing the intestines, as above, the fish were laid on their sides on a plank, but not in contact with one another. The day was humid and foggy, the temperature ranging from 69° at 8 a. m., and 72° at 12 m., to 71° at 5 p. m. At the end of 24 hours the fish were examined. The squeteague were badly decomposed on the side next the wood; on the other side decomposition had not proceeded so far, although it had progressed to a considerable extent. In the body-cavity decomposition was evident, but it had not advanced very far. The bonitos were in much better condition, although they emitted an odor of putrefaction, the side on which they lay being most affected. The walls of the body-cavity also were in better condition than those of the squeteague. The experiment shows that the free circulation of air about fish retards the process of decay.

After the intestines had been removed from 12 squeteaque the fish were hung up by their tails and allowed to remain 24 hours. The weather was cloudy, and the temperatures were as follows: 8 a. m., 71°; 12 m., 74°; 5 p. m., 73°. The atmospheric conditions were less favorable than on the previous day, yet at the end of 24 hours the fish were found to be in much better condition than in any of the preceeding experiments. There was a decided odor of putrefaction from the outside of the fish, but the abdominal cavity and the muscles showed only slight evidences of decomposition. The fish were in as good condition as many fish found in our markets and generally sold as "fresh." The experiments thus far made show that early cleaning, free circulation of air, and thorough draining retard putrefaction.

Twenty-four living squeteague were decapitated, thoroughly drained, and then their intestines were removed. From another series of equal number the intestines only were removed. The 48 fish were packed in a box in close contact with one another. The weather and temperature conditions were practically the same as on the preceding day. At the end of 24 hours the fish were very soft and had a bad odor. Although the 24 which had been decapitated were in a better state of preservation than the others, all were unfit for use. Those in the top layer, where they were exposed to the air, were in early stages of decomposition. Those on the bottom, away from the air and moistened by the drip from those above, were in advanced stages of decomposition. The experiment indicates the importance of thorough drainage of the flesh by early decapitation. The presence of blood hastens decay.

In all the above experiments the fish were taken from the fish-trap alive, and were immediately prepared to meet the conditions of the various experiments. By this means no decomposition could have taken place before the experiments were begun. The fish were handled as carefully as practicable, to prevent bruising or rupture of the muscular tissue. Cleanliness was assured through copious washing with sea water.

To recapitulate, the experiments show:

(*a*) That putrefaction takes place more rapidly if the viscera are not removed.

(*b*) That moisture hastens the process of decay.

(*c*) That the free access of air retards putrefaction.

(*d*) That drainage of the blood retards putrefaction.

(*e*) That if the head and intestines are removed, and if the fish is suspended by the tail so that the blood is drained from the entire body, the fish will remain sweet for a considerable time without the use of ice.

In none of the above experiments were putrefactive bacteria *prevented from entering the flesh* or directly hindered in their action after entrance. Consequently, further investigations were made to determine the feasibility of delaying bacterial invasion. To do this the fish must be *washed* with a solution which retards the growth of bacteria and is not injurious to the food qualities of the flesh. Various solutions were tried, but only one with success. In all cases control experiments were made on fish taken at the same time and subject to the same conditions, the only difference being that the control fish were not treated with the sterilizing fluids.

(1) The first experiment was with a 0.1 per cent solution of salicylic acid in sea water. 24 squeteague, taken alive from the nets, were carefully dressed, washed with this solution, packed in a box, and allowed to remain for 24 hours. The temperature ranged from 73° to 76°. When examined the next morning there was a perceptible odor of putrefaction; the fish were soft and unfit for market. The control fish were not much worse. Similar experiments were subsequently made with the same solution, but none were successful.

(2) The next preparation experimented with was a 10 per cent solution of potassium nitrate. 18 squeteague, cleaned immediately after being taken from the nets, were decapitated and thoroughly washed with this solution, and packed close together in a box. During the next 24 hours the weather was foggy, and the temperature ranged from 73° to 74°, at the end of which time decomposition had advanced to such a stage that the fish were totally unfit for shipment. There was no appreciable difference between the fish subjected to the potassium nitrate and those of the control experiment. Six more trials were made with this solution, but always with the same result.

(3) A 5 per cent solution of formalin was next used, but, as might have been predicted, the fish did not keep, and they were as bad at the end of 24 hours as those of the control.

(4) The next and most successful experiment was made with a 3 per cent solution of boric acid (B_2O_3) in sea water. 24 squeteague were dressed immediately after being caught, some decapitated, and others packed without removal of the head and gills. All were merely washed in the above solution and then closely packed in a box. The weather was foggy and cloudy, the temperature ranging from 74° to 83°. When examined 24 hours later the fish were in good condition, without odor, and decomposition had evidently not begun; the flesh was hard and firm, the eyes clear, and in fact one of the fish was declared by a native fisherman to have been taken from the water that very morning, and he was not readily convinced that it had been kept without ice for 24 hours. One of the squeteague was baked and served on my own table, and was pronounced excellent. It is needless to say that the control fish were in advanced stages of putrefaction and wholly unsuitable for food.

In these experiments with boric acid the fish were in no sense "embalmed," injected, or even preserved. The walls of the abdominal cavity, after the removal of the viscera, were simply washed with a sponge that had been dipped in the solution. The success of the experiment is of course largely dependent upon (*a*) the immediate removal of the viscera after the capture of the fish; (*b*) the careful handling of the fish, both before and after evisceration; (*c*) the thoroughness with which the walls of the abdomen are washed, and (*d*) the care with which the fish are packed. The use of boric acid will not prove satisfactory if fish are first thrown about, walked upon, carelessly eviscerated, washed in the sterilizing fluid, and then pitched into barrels. Those who prefer to abuse fish in this way will do well to stand by the older and more expensive methods—use ice, and complain of the market.

Mr. E. G. Blackford, one of the largest wholesale dealers in New York, has said:

> As an example of increased returns to the shippers from careful handling, I call attention to the fact that certain shipments of shad going to the New York market from North Carolina bring from 25 to 40 per cent more than other shad from the same locality. * * * What I wish to impress upon the shippers and fishermen is that for every dollar invested in labor and ice in packing the fish they will receive ten dollars in return.

Twenty more experiments were made with the same solution. Some of the animals were decapitated and others were not, but the swim bladders and kidneys were removed from all. If the gills were thoroughly washed in the solution it was found that even fish with the head attached kept as well as those which were decapitated. Nevertheless, in fish treated with boric acid putrefaction first appears in the gills. A bushel of squeteague prepared in this way was put on the deck of the U. S. Fish Commission schooner *Grampus* on the morning of August 12, 1898, and remained exposed to the sun throughout the day; the next morning, when cut up for bait, they showed no sign of decomposition. On another trip, 1,000 pounds of tile-fish were washed in the solution and then packed in ice, where they remained for two weeks; when unpacked they were in a perfectly fresh condition.

It is evident, then, that this solution retards the initial stages of putrefaction, even at the summer temperatures, and for a sufficient time for the fish to arrive at the market, where they may be iced and kept indefinitely. The solution of boric acid thus used is *not a preservative*, and it is not intended as such, but, like soap, it is an *agent of cleanliness*. As the fish are simply sponged over, the amount of the fluid that remains on a single fish is inconsiderable, and careful analysis fails to show more than the least trace in the flesh. Moreover, Chittenden and Gies have shown that boric acid given in doses, even up to 3 grams per day, has no effect upon proteid metabolism or on the nutrition of the body; that it is not cumulative, but is quickly eliminated from the system, and that it produces no renal complications. Its employment, therefore, as above recommended can have no injurious effect on the consumer.

In preventing the growth of the micro-organisms which cause putrefaction we also eliminate the cause of ptomaine formation. Though some of the ptomaines are exceedingly poisonous, this is not characteristic of all, and it can be safely stated that the greater number of those that have been isolated are of a nonpoisonous nature. The kind of ptomaine formed depends on the kind of micro-organism which produces it, the character of the material acted upon, and the circumstances in which putrefaction takes place. As the ptomaines are only transition products, representing mere temporary stages in the great process of decomposition by which the complex organic molecule is transformed into the simple inorganic state, it is evident that the kind of ptomaine present in putrid fish depends on the stage of putrefaction. Ptomaines formed when putrefaction takes place in free atmosphere will differ from those resulting from putrefaction where atmosphere is excluded. Almost any illness caused from infected food is spoken of as being due to "ptomaine poisoning," but in the majority of cases the poisonous bacterial products are not basic, though their true chemical structure is not understood.

It is worthy of note in this connection that poisonous ptomaines do not begin to appear until about the seventh day of putrefaction, and that they finally disappear if putrefaction is allowed to go on for a considerable time. The toxicity of the ptomaines themselves is not affected by cooking, no matter how thorough this may be. It should also be noted that there are two distinct kinds of poisoning that may arise from the use of fish as food. The first is an intoxication caused by the devouring of meat which has become invaded by ptomaine-producing bacteria. The second is an intoxication brought about by fish not necessarily infected with bacteria, but in which the poisons are *leucomaines* produced by the tissues of the fish and their normal product.

The researches of Meisener, Rosenbach, G. Hauser, F. Jahn, J. von Toder, and others have shown that the blood and flesh of healthy animals are entirely free from bacteria. But the contents of the digestive organs are rich in schizomycetes. Popoff has shown that the digestive canal of a healthy new-born animal is, at the moment of birth, free from bacteria. These, however, subsequently obtain access, principally in the food, and the contents of the bowels become extremely rich in microbes.

If a slaughtered animal is left without being disemboweled, these bacteria will make their way from the alimentary tract through the capillary vessels of the intestinal villi into the arterioles, the alkaline contents of which (rich in albumen) are especially favorable to these acidly putrefactive bacteria, so that the entire carcass quickly begins to undergo decomposition. This early decay may be prevented by the immediate removal of the entire alimentary canal, from esophagus to rectum, and if this precaution is taken the flesh (as already shown) will for a time remain free from putrefactive bacteria. If putrefaction afterwards sets in, it is probably due to bacteria from external sources which have obtained access to the flesh.

The gradual penetration of bacteria by way of the blood vessels into the interior of the flesh has been studied by Trombetta and Gartner. Gartner found them in the external layers only of meat 3 days old, but at the end of 7 days they had penetrated 2 cm. below the surface. It is probable, however, that the flesh of fish is not so resistant to the penetration of bacteria. The sources of this bacterial infection can not be entirely removed, but they can be considerably reduced by cleanly procedure, as above recommended, and attempts may be made to restrict the increase of the microbes and thus arrest the process of decay. The most common remedy is cold, but experiment has shown that the temperature must be kept some degrees below freezing to obtain the best results. This method is used not only in the American and Australian abattoirs, but haddock caught in Norway are cleaned and frozen at —50° C. and then shipped in specially constructed steamers. This freezing of fish does not immediately kill the bacteria present, for Koch has found very many bacteria in fish treated in this way, but it prevents the reproduction of the bacteria for the time being.

Foster has found that certain germs increase in meat stored at moderately low temperatures, though actual putrefaction is not produced by them. Moreover, the researches of Frænkel, Bordoin, Uffreduzzi, Prudden, and Heyroth show us that natural ice may contain both putrefactive and pathogenic bacteria. This fact alone should teach us to look with suspicion upon any meat that has been brought in direct contact with ice of unknown origin, especially when the ice is allowed to melt so that the drip soaks into the flesh.

THE CHEMICAL COMPOSITION OF THE SUB-DERMAL CONNECTIVE TISSUE OF THE OCEAN SUNFISH.

By E. H. GREEN.

U. S. Fish Commission Bulletin for 1899.

U. S. COMMISSION OF FISH AND FISHERIES,
GEORGE M. BOWERS, Commissioner.

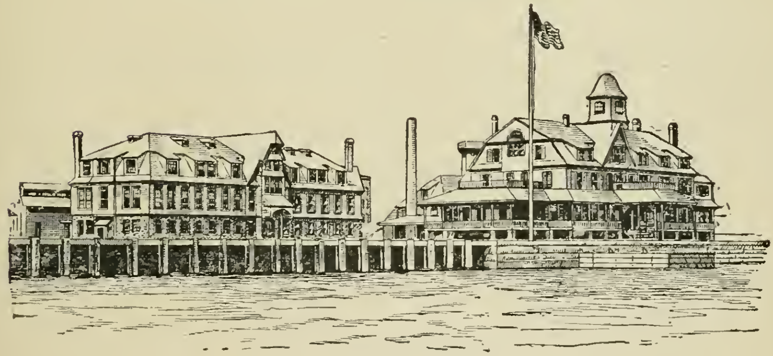
CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION, WOODS HOLE, MASSACHUSETTS.

THE

CHEMICAL COMPOSITION OF THE SUB-DERMAL CONNECTIVE TISSUE OF THE OCEAN SUN-FISH.

BY

ERIK H. GREEN, A. M.



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THE CHEMICAL COMPOSITION OF THE SUB-DERMAL CONNECTIVE TISSUE OF THE OCEAN SUN-FISH.

BY ERIK H. GREEN, A. M.

The tissue under examination was obtained from a sun-fish * taken near the laboratory of the United States Fish Commission at Woods Hole, and at the time the study was undertaken had been preserved in alcohol for nearly a year. The preserved fragments were of a creamy white color, homogeneous, very tough and inelastic, and under the microscope were found to consist almost entirely of elastic-like fibers. As no reference to the chemical composition of this substance could be found, the following analyses were undertaken to determine (1) whether the tissue was composed wholly of elastin, and (2) what was the essential constituent if the tissue was found not to be composed of elastin.

The analyses were conducted as follows: A few grams of the alcoholic tissue were cut into small fragments, rinsed in water, and dried at 110° C. When dry the fragments were of yellow color, semitransparent, hard, and brittle. They were insoluble in hot or cold 10 per cent sodium carbonate, but cold 50 per cent acetic acid caused them to swell enormously, although they did not dissolve. The dry fragments were soluble in strong potassic hydrate, in hot 1 per cent potassic hydrate after one hour, in cold 7 per cent potassic hydrate after two hours, and in the hot 7 per cent potassic hydrate were dissolved in a few minutes. Deflagrated with soda and niter they showed the presence of sulphur and of a trace of phosphorus.

The alcoholic tissue was insoluble in ammonia (sp. gr. 0.955), in lime water, in cold 1 per cent hydrochloric acid, and in hot or cold 10 per cent sodium carbonate. It was slowly soluble in boiling water, cold 10 per cent hydrochloric acid, cold 1 per cent potassic hydrate, and glacial acetic acid. It was readily soluble in strong hot hydrochloric acid, and nitric acid, in cold potassic hydrate (14 per cent), and in hot 5 per cent potassic hydrate.

A characteristic of collogen is its property of gelatinization. To test this property in the tissue under examination, the following experiments were made: About 50

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* The sun-fish, *Mola mola* (Linnæus), is found on the Atlantic coast, in summer as far north as the Newfoundland Banks. It occurs in such numbers that ten or more may be seen in a single day, the large black dorsal fins elevated above the surface of the water betraying the presence of the animals as they drift leisurely along. Their total unfitness for food and their pelagic life have rendered them safe from the persecutions of the fishermen, and not only are they abundant, but the individuals attain to enormous size. Specimens 7 or 8 feet in length weigh several hundred pounds. A very large percentage of the weight of each individual is made up of a firm tissue superficially resembling blubber, but not oleaginous. By the following chemical analyses this tissue, heretofore considered worthless, is shown to yield collogen, an albuminoid, which is the basis of all glues and gelatins. The fish are thus shown to have considerable commercial value.—H. C. BUMPUS.

grams of the finely divided and well-washed tissue were boiled for 6 hours in half a liter of distilled water, the water being renewed as it evaporated. The tissue almost completely dissolved, and the yellowish solution on cooling became somewhat viscid, but it did not gelatinize, even when evaporated to a volume of only 100 c. c. The concentrated solution was diluted and filtered. It was neutral to litmus, was precipitated by phosphotungstic acid, and by phosphomolybdic acid; the precipitates were insoluble on heating, but were soluble in potassic hydrate. When precipitated by Millon's reagent the precipitate was soluble in excess of reagent. When precipitated by tannic acid, by metaphosphoric acid, absolute alcohol, and mercuric chloride in presence of free hydrochloric acid the precipitates were insoluble.

The solution gave no precipitate with acetic acid and potassium ferrocyanide, neutral or basic acetate of lead, alum, cupric sulphate or acetate, ferric chloride, sodium orthophosphate, or mercuric potassium iodide. It was not blackened when boiled with lead acetate and potassic hydrate. It gave a strong biuret reaction, and on boiling did not reduce copper. Hot concentrated sulphuric acid and glacial acetic acid produced no violet coloration. Hot strong nitric acid gave no precipitate or coloration, but subsequent addition of ammonia caused a deep orange tint. Saturated with ammonium sulphate, the solution gave a copious precipitate, which floated on the surface of the liquid, forming a coagulum-like layer. Picric acid in saturated solution produced a light-yellow precipitate, insoluble in excess of the reagent, soluble in hot, insoluble in cold water. On shaking, a stiff coagulum formed above the subnatant clear liquid, so that the test tube could be inverted without loss of its contents.[1]

To a few centimeters of the original solution, several drops of formaldehyde (40 per cent solution in water) were added, and the whole evaporated to dryness. The residue was insoluble in hot or cold water. It had become apparently formogelatin.

The reactions given above show that true proteids, also chondrin, are absent, or present in quantities too small for detection. All the phenomena, especially the peculiar and characteristic reactions given by picric acid, ammonium sulphate, and formaldehyde, point to the presence of gelatin, notwithstanding the fact that the solution did not gelatinize and that the original tissue was soluble in dilute potassic hydrate. Elastin can be present only in traces, if at all, since it is insoluble in boiling water, even after 96 hours' boiling,[2] and insoluble also in 1 per cent potassic hydrate,[3] which dissolves the tissue under consideration.

The following experiments were made to determine whether other substances were present with the collogen-like albuminoid.

Several grams of the alcoholic tissue were cut up, washed, and treated with cold 5 per cent potassic hydrate. After 24 hours the tissue was almost wholly dissolved; the solution was filtered, slightly acidified with acetic acid, and submitted to the following reactions. Phosphotungstic acid gave a precipitate soluble on heating, and phosphomolybdic acid, tannic acid, and metaphosphoric acid also gave precipitates. The solution was not precipitated by acetic acid and potassium ferrocyanide, nitric acid, basic or neutral lead acetate, or copper sulphate, and it gave a strong biuret reaction. There was no coloration with hot sulphuric and glacial acetic acid. The fact that the precipitate given by phosphotungstic acid is soluble by heating shows, according to the researches of Mallet,[4] that true proteid substances can not be present in the solution; for proteid substances, including gelatin and chondrin and excepting peptones, give precipitates insoluble on heating. In testing the boiling-water solution of the tissue as given before, the phosphotungstic acid precipitate was found to be insoluble on heating.

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[1] Allen and Tankard's test for gelatin. Allen's Com. Organ. Analysis, vol. IV, 1898, p. 469.

[2] Chittenden and Hart. Zeit. für Biologie, 7 Bd., s. 369—(abs.—Horbaczewski Zeit. für Phys. Chemie, Bd. 6, s. 330.)

[3] Ibid.

[4] U. S. Dept. Agric., Division of Chem., Bull. 54, 1898, pp. 20–21.

The behavior of the substance with digestive fluids was as follows: (A) Fragments of the tissue were rapidly digested at 40° C., when treated with a pepsin hydrochloric acid solution. (B) When treated with an alkaline trypsin solution, the fragments were attacked with extreme slowness. For this experiment about 40 grams of the alcoholic tissue were cut up fine, well washed to remove excess of alcohol, and then treated with a 0.5 per cent sodium carbonate solution of pancreatin, to which a few fragments of thymol were added. The temperature was kept at or near 40° C. After four days the tissue had been only slightly attacked, but at the end of eight days it was almost completely dissolved. When boiled in water (for 10 minutes) and then subjected to the action of the trypsin solution, the fragments were dissolved almost completely in 24 hours. The same result was obtained by first swelling the washed tissue fragments in dilute acetic acid and then submitting them to digestion. The behavior of the subdermal connective tissue toward digestive fluids seems to identify it with collogen, the basis of bone, cartilage, and other gelatine-yielding substances of the body. True collogens are wholly unaffected by tryptic digestion, unless they have been heated previously with water or swelled with acids.[1]

QUANTITATIVE ANALYSIS.

A preliminary analysis was made to determine the percentage of nitrogen, sulphur, and ash in the dried alcoholic tissue. No attempt was made to estimate the amount of phosphorus, since the qualitative examination showed only mere traces of this element. In this, as in the following analysis, the nitrogen was determined by the Gunning modification of the Kjeldahl method, using mercuric oxide as an oxidizing agent, and cochineal as an indicator in the back-titration. Sulphur was estimated as barium sulphate in the usual way, after fusion of the tissue with sodium carbonate and potassium nitrate. Carbon and hydrogen were determined as usual by combustion with cupric oxide, a zone of lead chromate being placed after the oxide to arrest any sulphur dioxide present.

About 50 grams of the alcoholic tissue were cut up, dried for several days at 90° C., pulverized and redried at 110° C., to constant weight. Analysis of this dry substance gave the following results:

Quantity of substance (grams).	Constituents.					
	Ash.		Nitrogen.		Sulphate of barium.	
	Grams.	Per cent.	Grams.	Per cent.	Grams.	Per cent of sulphur.
1.5040	.0221	1.47	....	....	....	....
.8162	....	....	.1337	16.37	....	....
.2829	....	....	.04746	16.77	....	....
.2414	....	....	.04032	16.70	....	....
.2065	....	....	.03458	16.71	....	....
.6498	....	....	....	....	.0245	.53
.6836	....	....	....	....	.0206	.42
Mean	....	1.47	....	16.64	....	.47

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[1] Hoppe-Seyler.—Handbuch d. Phys. u. Path. Chem. Analyse, 6 Auf., s. 270.

These results shed no light on the proteid composition of the tissue, except that the percentage of nitrogen corresponds almost exactly to that given by Chittenden and Hartwell[1], for the nitrogen in elastin prepared from the neck bands of cattle. This fact has little weight, however, in view of the high percentage of ash present in the tissues under consideration.

About 50 grams of the tissue were reduced to fragments, and washed repeatedly, by decantation, with cold water. The fragments were then washed with 90 per cent alcohol for 24 hours, and allowed to stand under ether, with frequent shaking, for 36 hours. The material was then removed, freed from excess of ether, and dried in the air bath at 110° C., to constant weight. The dry fragments were tough and leathery, and could not be powdered. A portion gave with Millon's reagent a light pinkish color. Analysis of this dried substance gave the following results:

Quantity of substance (grams).	Constituents.							
	Water.		Carbon dioxide.		Nitrogen.		Ash.	
	Grams.	Per cent of hydrogen.	Grams.	Per cent of carbon.	Grams.	Per cent.	Grams.	Per cent.
.3229	.1988	6.84	.5704	48.18	....	....	.0013	.40
.3658	.2227	6.75	.6476	48.28	....	....	....	....
.3381	....	....	....	....	.06146	18.17	....	....
.4695	....	....	....	....	.08568	18.25	....	....
Mean	....	6.80	....	48.23	....	18.21	....	.40

By difference, oxygen + sulphur = sum of means from 100 = 26.36 per cent.

The high percentage of nitrogen shows at once that the tissue is not composed of elastin. Both the carbon and the nitrogen determinations would indicate that the tissue is a collogenous substance, and under appropriate treatment it has yielded glue of excellent quality.

BROWN UNIVERSITY, *Providence, Rhode Island.*

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[1] Abs.—Allen. Com. Organ. Analysis, vol. IV, 1898. [Appendix.]

THE GAS-BUBBLE DISEASE OF FISH AND ITS CAUSE.

By F. P. GORHAM.

U. S. Fish Commission Bulletin for 1899.

U. S. COMMISSION OF FISH AND FISHERIES,
GEORGE M. BOWERS, Commissioner.

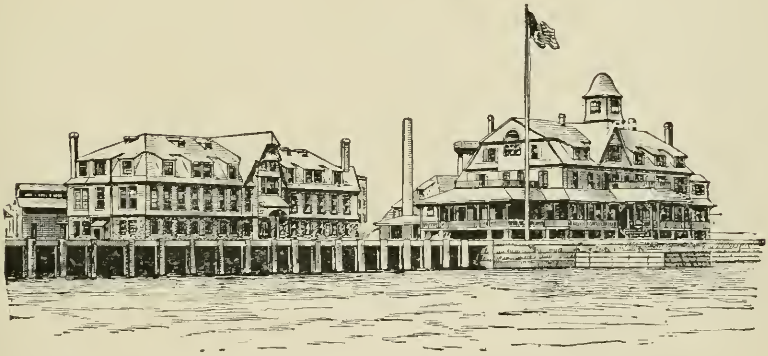
CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE U. S. FISH COMMISSION, WOODS HOLE, MASSACHUSETTS.

THE

GAS-BUBBLE DISEASE OF FISH AND ITS CAUSE.

BY

F. P. GORHAM, A. M.,
Assistant Professor of Biology, Brown University.



Extracted from U. S. Fish Commission Bulletin for 1899. Pages 33 to 37. Plate 12.

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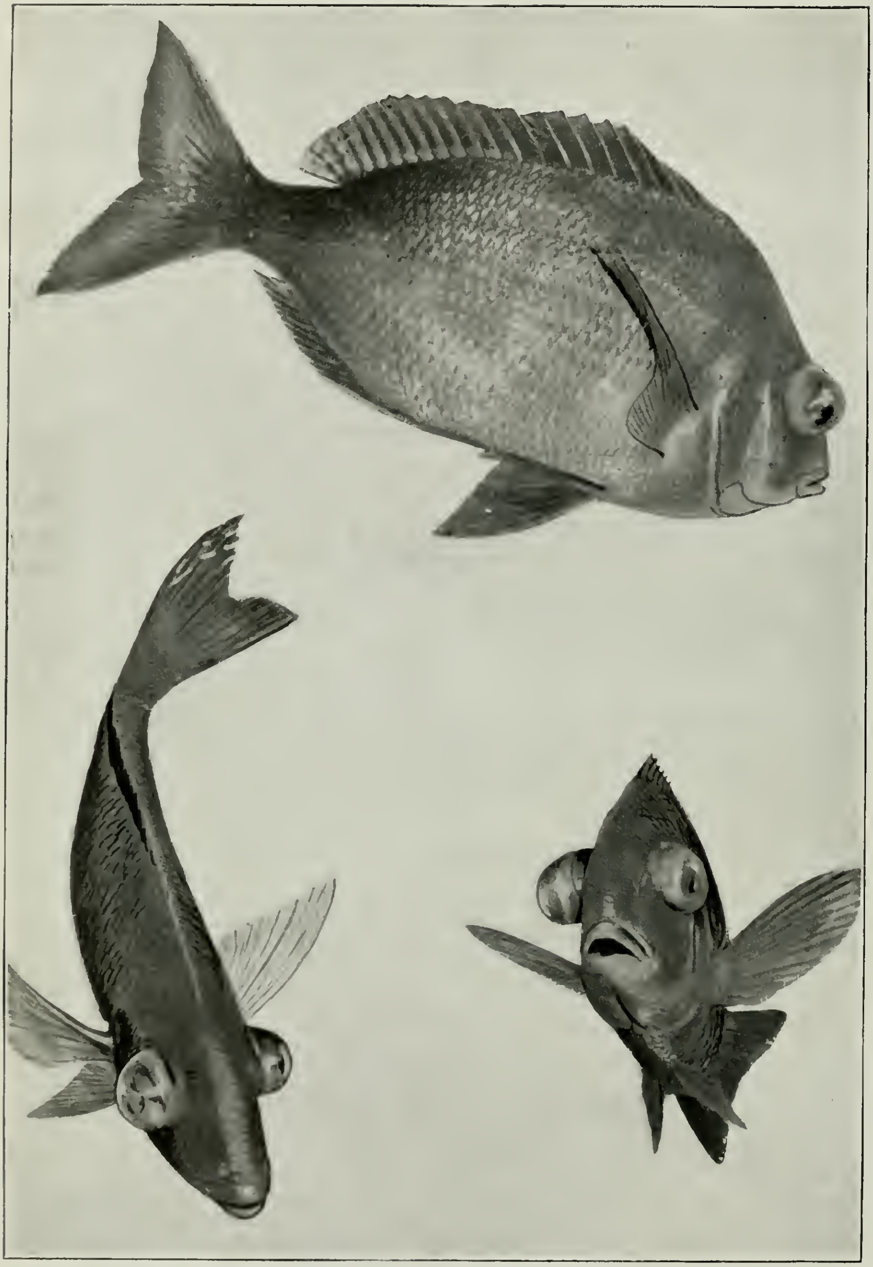

SCUP (*Stenotomus chrysops*). Three views of the same fish taken while alive in the aquarium of the United States Fish Commission at Woods Hole, Mass

Contributions from the Biological Laboratory of the U. S. Fish Commission,
Woods Hole, Massachusetts.

THE GAS-BUBBLE DISEASE OF FISH AND ITS CAUSE.

By F. P. GORHAM, A. M.,
Assistant Professor of Biology, Brown University.

For several years it has been noticed that many salt-water fish when kept in aquaria develop, after a longer or shorter period, a disease which is first manifested in the formation of vesicles of gas on the fins or other parts of the body. These vesicles gradually increase in size and number, and finally invade all superficial parts of the animal. The fins, one after another, become affected, and the vesicles frequently form in the eyeball, beneath the cornea, or in the loose connective tissue of the orbit, so that the eyes are forced from their sockets; less frequently the bubbles gather beneath the mucous membrane lining the mouth and gill-arches, or beneath the integument, particularly along the lateral line, so that the scales are raised from the surface. The presence of these vesicles often disturbs the equilibrium of the fish so that it swims about with its head elevated, or, more frequently, directed downward or tilted to one side.

The disease has been noticed only in fish kept in the aquaria. It has not been found in specimens taken from the sea, nor has it been observed in fish kept in "cars" in deep water, nor in those retained in "pounds," the water of which is from 6 to 12 feet in depth. The affected fish live a shorter or longer time after the vesicles begin to appear, some succumbing in a few hours, others resisting the disease for several weeks. Young "puffers" usually die in less than 24 hours after being placed in the aquaria, but several scup lived for weeks after their eyes had actually dropped from their sockets.

The following fish were affected by the disease during the spring and summer of 1898, and the list includes all the fish, with two exceptions, which were kept in the aquaria of the Fish Commission at Woods Hole, Mass., from March to September:

Common name.	Scientific name.	Bathymetric range.
		Fathoms.
Winter flounder	Pseudopleuronectes americanus	1 to 30
Summer flounder	Paralichthys dentatus	1 30
Hog choker	Achirus fasciatus	1 30
Tautog	Tautoga onitis	1 30
Tomcod	Microgadus tomcod	1 15
Squirrel hake	Urophycis tenuis	1 300
Hake	Urophycis chuss	1 150
Sea-robin	Prionotus carolinus	5 80
Sea robin	Prionotus strigatus	5 80
Puffer	Spheroides maculatus	2 10
Toad-fish	Opsanus tau	1 8
Stickleback	Gasterosteus bispinosus	1 5
Cunner	Tautogolabrus adspersus	1 35
Pipe-fish	Siphostoma fuscum	1 100
Sea bass	Centropristes striatus	1 40
Butter-fish	Rhombus triacanthus	3 10
Rudder-fish	Palinurichthys perciformis	1
Scup	Stenotomus chrysops	2 20

The following invertebrates showed signs of the disease: Squid, naked mollusks, scallops (*Pecten tenuicostata*), hydroids (*Parypha crocea*). Squid egg-sacs and some of the green algæ also developed internal bubbles apparently of the same nature.

Minnows (*Fundulus heteroclitus* and *Cyprinodon variegatus*) and skates (*Raja erinacea*) in no case were affected.

In most fish the disease manifests itself first on the fins, but in the scup it attacks the socket of the eye and gradually forces the eyeball from the orbit (plate 12). In the adult puffer the dorsal fin is first attacked; in the young puffer the base of the tail. In the pipe-fish the bubbles appear about the snout and later spread to other parts of the body. In young winter flounders (about 1 centimeter long) the body cavity frequently contains a large bubble.

The disease is not confined to the aquaria at Woods Hole. Mr. L. B. Spencer, who is in charge of the Battery Park Aquarium in New York City, writes me that he has noticed it there for several years.

From the appearance of the fish, from the rapid development of the disease in fish introduced into the aquaria, and from the nonappearance of the disease in fish outside of the aquaria, it at first seemed to me that the aquaria had become infected with some disease-producing organism, that the organism was a "gas producer," and that it spread rapidly through the tissues of the fish and produced the gas which collected as bubbles in various parts of the body. With this idea in mind the task of finding, isolating, and studying the organism was begun.

All of the tissues of the fish were searched thoroughly for foreign organisms; hundreds of cultures were made on the ordinary and also on special media, such as fish-bouillon, fish-gelatin, and fish-agar. The cultures were kept warm, cold, and at the temperature of the water in the aquaria; cover-glass "smears" were repeatedly examined; but all to no purpose. Not a sign of any pathogenic organism was found. The only pathological change noticed in the tissues was a remarkably emphysematous condition of epidermis, muscles, connective tissue, fat, etc., in the neighborhood of the vesicles. I became convinced that the disease could not be attributed to the invasion of micro-organisms.

Two phenomena suggested a new line of inquiry: (1) None of the small shallow-water fish developed bubbles; (2) the deep-sea fish when brought to the surface by line or dredge often show a protrusion of the eyes and an expansion of the tissues, comparable to the conditions under consideration. Could not the disease be the direct result of the reduction of pressure upon the tissues of the fish, a reduction which must occur when animals habituated to a life in deeper water are compelled to live in the shallow water of the aquaria?

To answer this question the following experiment was made: Several young scup were placed in water in a flask; the air was then exhausted from above the water, thus reducing the pressure. As soon as the pressure was at all diminished, the fish immediately sought the bottom of the flask, heads down, and made every effort to seek deeper water and thus regain their normal pressure. By their continued struggles they soon became exhausted and came to the surface. The atmospheric pressure was then restored and they became quiet and swam about naturally. The reduction of pressure was repeated three or four times at intervals of 30 minutes. After the experiment the eyes of the fish showed well-developed bubbles. The experiment was repeated on the following day, with the same fish, with the result that the bubbles enlarged until the eyes began to protrude.

Other experiments, indicated in the following table, were made:

Fish.	Total length of time subjected to reduction of atmospheric pressure.		Results.
	Hrs.	*Mins.*	
Scup (5 cm. long)	1	0	Bubbles in eyes.
Same fish	1	0	Bubbles enlarged; eyes protrude.
Scup (5 cm. long)	1	12	One eye shows bubbles and hemorrhage.
Sea-robin (6 cm. long)	3	49	Bubbles on pectoral fin and on "feelers."
Sea robin (6 cm. long)	0	14	Bubbles on lower jaw.
Puffer	4	4	Bubbles on tail.
Minnow (*Cyprinodon variegatus*)	6	0	No change.

Normal fish were kept as controls in all cases and showed no change. Whenever scup were subjected to this reduction their eyes were affected first; bubbles formed and the eyes protruded in much less time, but in exactly the same way as in scup placed in the aquaria. In the young sea-robins bubbles appeared on the pectoral fins and on the finger-like appendages, while in the young puffers they appeared at the base of the tail. In all these cases the parts first affected were the same as those subject to the disease in the aquaria. The minnows unaffected in the aquaria were unaffected by the removal of the atmospheric pressure.

Now, the question naturally arises, will the increase in pressure improve the condition of the fish already suffering from the disease? Small scup taken from the aquarium, already showing protrusion of the eyes and bubbles on the head and fins, were subjected to a pressure equal to 16 feet of water. In 24 hours many of the bubbles had disappeared, and the eyes had returned to their normal condition. Under this treatment puffers recovered from a decidedly diseased condition in 24 hours. The data of these experiments may be tabulated as follows:

Fish.	Length of time subjected to pressure of 16 feet of water.	Results.
	Hours.	
Scup with bubbles on head	24	Bubbles disappeared.
Scup with protruded eye	24	Eye nearly normal.
Scup with bubbles on head and protruded eye	24	Entirely normal.
Puffers (3.5 cm. long). Bubbles at base of tail	24	Do.
Puffer (3.5 cm. long). Bubbles on dorsal fin	24	Normal.
Puffer (3.5 cm. long). Bubbles on eye and on fin	24	Eye nearly normal. Bubbles on fin disappeared.
Puffer (3.5 cm. long). Large bubble under right fin.	24	Normal.

Control animals checked the results of these experiments.

In both the reduced and the increased pressure experiments above tabulated young fish were used, but whenever adult animals were employed similar results were obtained.

The change in pressure which fish must undergo when transferred from the ocean to aquaria is not small in amount. We have only to consider that at the surface the pressure is about 14.7 pounds per square inch, and that for every foot in depth it increases at the rate of 0.445 pound per square inch. At a depth of 5½ fathoms the pressure is just double that at the surface, and at a depth of 300 fathoms it would amount to over 800 pounds.

Now, as may be seen by referring to the table of the depths from which the fish under consideration were taken, a reduction of pressure must take place when fish are confined in shallow aquaria. Their tissues relax under the reduction, and any gas present must expand. Since, according to the law of the expansion of gases, a volume of gas occupies just twice the space at the surface that it does at 5½ fathoms, a fish drawn from 300 fathoms to the surface must suffer an expansion of its contained gases to over 54 times their original volume.

Gas is present in all fish, in the alimentary tract, in the air bladder, and in the blood and other fluids of the body. As this gas expands and seeks an outlet the tissues are loosened and torn apart; the intestine and air bladder are greatly distended and perhaps ruptured, the circulation of the blood is impeded or stopped, and vesicles of gas form in various parts of the body.

These phenomena have been noticed for a long time in fish taken from great depths. Such fish are usually dead when they reach the surface, their eyes are protruded, their air bladder is ruptured, their intestines are everted from mouth or anus, and their scales are often lifted from the skin. The greater the depth from which they come the more pronounced are the changes. So great is the pressure to which some of the deep-sea fish are subjected (*Melamphaes beanii* from 2,949 fathoms sustains a pressure of 3.9 tons per square inch), that the structure of the bones, connective tissues, and muscles is peculiarly modified. Even in fish taken from 15 or 20 fathoms one may note the protrusion of the eyes, the eversion of the intestine, and the noise of the expanding gas working through the tissues.

We are thus led to the conclusion that the "gas bubble disease" is caused by a reduction of pressure. Naturally, the disease has never been noticed except in the aquaria; normally shallow-water fish are never affected, and the greater the normal depth of a fish the more severely is it affected. Occasionally certain deep-water fish voluntarily seek the surface, but it is only when they can not return to deeper water that the changes brought about by the expansion of gases become evident.

It is interesting to compare these changes in fish with those observed in higher animals when subjected to alterations of pressure. Animals at the surface of the earth are subjected to an atmospheric pressure of about 14.7 pounds per square inch. When this pressure is diminished or increased, physiological changes result. Mountain climbers, at an elevation of 2 miles, suffer from increased rapidity of respiration, quickened pulse, painful, throbbing headache, flow of blood from the nose, eyes, and mouth, nausea, and vomiting. On the other hand, when the pressure is increased to from 50 to 60 pounds per square inch, as in caissons, workmen experience an annoying sensation about the tympanum, an irritation of the skin called the "puces," an alteration of the voice, deep, slow, and easy respiration, active digestion, an absence of thirst, and an increased secretion of saliva and urine. Return to normal pressure has the same effect as going into rarefied air. The "puces" is replaced by a chill, respiration becomes difficult, the pulse is rapid and hard, there are pains in the joints and muscles, and persistent cramps, paralysis, and coma are frequent; death may result in a few minutes. In such cases autopsies have shown congestion of the viscera, emphysematous spots on the lungs, and other indications that the blood contained bubbles of gas.*

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*I am indebted to Mr. Frederick T. Lewis for calling my attention to these facts. See "The physiological effects of compressed air," in the Boston Medical and Surgical Journal, October 6, 1898.

Experiments have shown that under compressed air the amount of oxygen absorbed by the blood increases with the pressure, according to the law of the absorption of gases. It may be the liberation of this oxygen and other gases under reduced pressure that causes death in the above cases.

In recording experiments upon the influence of high pressures upon various animals, Monsieur P. Reguard says: *

> A fish without an air bladder, or one in which the air bladder has been emptied of gas, can be submitted to a pressure of 100 atmospheres, 1,470 pounds per square inch, without injury. When the air bladder is not emptied a very curious phenomenon is observed. Under pressure of several atmospheres the gas of the air bladder dissolves in the blood, and at the moment of decompression it suddenly becomes disengaged in the blood vessels, forming a foam which stops all circulation, and the animal dies; for thé same reason fish drawn from the depths of the sea are dead when they reach the surface.

The bearing of this matter of pressure on geographical distribution should be considered. It might seem that there are no barriers to universal distribution in the sea save those indicated by the isotherms, but the isobars must indicate the location of effectual barriers for certain species.

Since even slight changes of pressure are detrimental, and each fish swimming in the sea tends to remain at about one level, it is reasonable to suppose that when a fish leaves this level the difference of pressure becomes uncomfortable and there is a tendency for it to return to its normal habitat. The air bladder is at present considered not an organ under the influence of the muscles of the fish, by means of which it alters its specific gravity, but rather a delicate gauge, which notifies the animal of changes of pressure above or below the normal.

Were a fish to pass too far beyond its normal depth, either up or down, the expansion or contraction of the gas of the air bladder would so change the specific gravity of the animal that its muscular activity would no longer be able to cope with the upward or downward tendency, and the fish would be carried to the surface or the bottom. Thus the very presence of an air bladder works the destruction of the fish. Cases are reported where deep-sea fish have come to the surface in this way, evidently having been carried too far from their normal level in struggles with their prey.

It is true that slight changes of level may be brought about by the secretion or absorption of gas by the walls of the air bladder. That the walls of the air bladder secrete and absorb gas has been shown by experiment. I have repeatedly emptied the air bladders of fish and found a small amount of gas secreted in 24 hours. But this process of secretion and absorption is relatively slow, and permanent changes of habitat could be brought about only very gradually; moreover, only very slight changes are possible for each species.

Thus we see that fish are surrounded by barriers of pressure, and that each species and probably each individual is constrained to remain at a certain level, and the restricted distribution of certain fish is thus explained.

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* Recherches experimentales sur l'influence des très hautes pressions sur les organismes vivants. Compt. Ren., XCVIII, March 21, 1884, p. 745.

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